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Interactions between climate, trembling aspen, and outbreaks of forest tent caterpillar in Alberta

by

Barry James Cooke ©

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of the requirements for the degree of Doctor of Philosophy
in
Environmental Biology and Ecology

Department of Biological Sciences

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Barry James Cooke
3971 NW 23 Circle
Gainesville, FL
32605
USA

Date: July 23, 2001

University of Alberta

Faculty of Graduate Studies and Research

The undersigned certify that they have read, and recommend the Faculty of Graduate Studies and Research for acceptance, a thesis entitled "Interactions between climate, trembling aspen, and outbreaks of forest tent caterpillar in Alberta" submitted by Barry James Cooke in partial fulfilment of the requirements for the degree of Doctor of Philosophy in Biological Sciences in Environmental Biology and Ecology.

Jens Roland.

Dr. Jens Roland

Stan Bout

Dr. Stan Boutin

SRLele

Dr. Subash Lele

W.J.A.Vo

Dr. Jan Volney

MRT Dale

Dr. Mark Dale

W. M. Hammond

for Dr. Andrew Liebhold

Date: July 20, 2001

Dedicated to the people of rural Alberta

ABSTRACT

Periodic outbreaks of the forest tent caterpillar, *Malacosoma disstria* Hbn., occur at six to sixteen year intervals throughout Canada, causing severe defoliation of host-trees. There are many environmental factors and natural enemies that influence survival and reproduction, but it is unclear how these conspire to produce large-scale synchronized population fluctuations.

A localized outbreak of forest tent caterpillars in central Alberta was monitored beginning in 1995. Populations started declining in 1995 and widespread collapse occurred during the summer of 1996. Many eggs failed to hatch in the spring of 1996, probably as a result of cold winter temperatures. Rates of parasitism were high in the spring and summer of 1996, and populations became scarce in 1997. Poor egg hatch in 1996 thus seems to have assisted in precipitating parasitism-driven collapse of this tent caterpillar population.

Historical outbreaks of forest tent caterpillar were reconstructed for the province of Alberta by measuring ring widths of sections of trembling aspen, *Populus tremuloides* Michx. Aspen ring width chronologies spanning the period 1837-1998 indicated a persistent pattern of decadal outbreaks. Outbreaks were less regularly periodic and less well-synchronized in Alberta than they appear to be in Ontario, but they were not chaotic. Outbreaks were more frequent, less well-synchronized, and less stable in the aspen parkland than in the boreal forest.

High-resolution outbreak reconstruction in the Cooking Lake area showed that decadal outbreaks are often split into spatially and temporally discrete pulses, such that

localized outbreaks occur at five to seven year intervals.

Boreal and parkland outbreak cycles were modeled as a stochastic host-parasitoid interaction perturbed by winter temperature. There was weak evidence that monthly winter temperature acts as a phase-locking or period-forcing mechanism on outbreak cycles. The effect of temperature, however, seems to be more complicated than this model assumes.

A theoretical model of spatiotemporal outbreak patterns at Cooking Lake suggested that sub-decadal outbreak asynchrony may be driven by forest fragmentation. Winter temperature may help to further de-synchronize outbreaks, but a better model is required to simulate the effects of daily winter temperature on egg survival and density-dependent susceptibility and vulnerability of eggs to winter-kill. A synthetic conceptual model is offered as a starting point.

PREFACE

This study uses a dendrochronological approach to reconstructing long-term patterns of forest tent caterpillar-caused defoliation of trembling aspen in Alberta, Canada. Spatial and temporal variation in outbreaks is explained in terms of a stochastic predator-prey interaction mediated by forest structure and fluctuations in winter temperature. Outbreak patterns in Alberta and Ontario are contrasted and a synthetic explanation for observed differences is conjectured.

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TABLE OF CONTENTS

CHAPTER .... **PAGE**

1. INTRODUCTION 1
- 1.1 Background 1
- 1.2 Objectives 12
- 1.3 Methodology 18
- 1.4 Broad relevance 23
- 1.5 Literature Cited 24

2. THE EFFECT OF SPRING WEATHER AND INSECT DEFOLIATION ON ASPEN GROWTH IN CENTRAL ALBERTA 49
- 2.1 Introduction 49
- 2.2 Methods 53
- 2.3 Results 65
- 2.4 Discussion 77
- 2.5 Conclusion 86
- 2.6 Literature Cited 87

3. DENDROECOLOGICAL RECONSTRUCTION AND ANALYSIS OF FOREST TENT CATERPILLAR OUTBREAKS ACROSS NORTHCENTRAL ALBERTA 125
- 3.1 Introduction 125
- 3.2 Methods 128
- 3.3 Results 138
- 3.4 Discussion 150
- 3.5 Conclusion 159
- 3.6 Literature Cited 161

4. SURVIVORSHIP BIAS IN DENDROECOLOGICAL RECONSTRUCTION OF FOREST TENT CATERPILLAR OUTBREAKS USING TREMBLING ASPEN 203
- 4.1 Introduction 203
- 4.2 Methods 205
- 4.3 Results 207
- 4.4 Discussion 208
- 4.5 Conclusion 211
- 4.6 Literature Cited 211

5. ARE FOREST TENT CATERPILLAR OUTBREAKS CHAOTIC? 219
- 5.1 Introduction 219
- 5.2 Methods 223
- 5.3 Results 227
- 5.4 Discussion 230

5.5 Conclusion 237
5.6 Literature Cited 238

6. WHERE, WHEN, AND WHY ARE FOREST TENT CATERPILLAR POPULATIONS IMPERFECTLY SYNCHRONIZED: MULTI-SCALE SPATIOTEMPORAL ANALYSIS OF OUTBREAKS IN ALBERTA ... 250
6.1 Introduction 250
6.2 Methods 259
6.3 Results 268
6.4 Discussion 288
6.5 Conclusion 305
6.6 Literature Cited 306

7. THE IMPORTANCE OF DETRENDING ERRORS IN SPATIOTEMPORAL DENDROECOLOGICAL DISTURBANCE RECONSTRUCTION 350
7.1 Introduction 350
7.2 Methods 358
7.3 Results 360
7.4 Discussion 361
7.5 Conclusion 363
7.6 Literature Cited 364

8. THE EFFECT OF WINTER TEMPERATURE ON FOREST TENT CATERPILLAR EGG SURVIVAL AND POPULATION DYNAMICS IN NORTHERN CLIMATES 374
8.1 Introduction 374
8.2 Methods 378
8.3 Results 380
8.4 Discussion 383
8.5 Conclusion 397
8.6 Literature Cited 399

9. ARE FOREST TENT CATERPILLAR OUTBREAK CYCLES INDUCED BY WINTER TEMPERATURE FLUCTUATIONS? 421
9.1 Introduction 421
9.2 Methods 422
9.3 Results 425
9.4 Discussion 427
9.5 Conclusion 431
9.6 Literature Cited 432

10. THE EFFECT OF LANDSCAPE HETEROGENEITY ON SPATIOTEMPORAL PATTERNING IN THEORETICAL HOST-PARASITOID MODELS 440
10.1 Introduction 440

10.2 Methods 442
10.3 Results 448
10.4 Discussion 451
10.5 Conclusion 452
10.6 Literature Cited 453

11. CONCLUSION 463
11.1 Executive summary of results 463
11.2 Summary of principal themes 463
11.3 Future research 476

APPENDIX 1. A DETAILED GUIDE TO THE PREPARATION OF ASPEN SAMPLES FOR DENDROCHRONOLOGICAL ANALYSIS 486

APPENDIX 2. A ZERO-COST METHOD FOR ANIMATING SPATIOTEMPORAL ECOLOGICAL DATA 489

APPENDIX 3. SPATIOTEMPORAL FACTOR ANALYSIS WITH ROTATED PRINCIPAL COMPONENTS 491

LIST OF TABLES

TABLE .... PAGE

Table 2.1. Regression coefficients and partial coefficient of determination for aspen ring width modeled as a function of spring precipitation and spruce ring width in two time periods. 103
Table 2.2. Regression coefficients and coefficient of determination for the full, partial, and step-wise reduced models of aspen ring width during the period 1957-1998. 104
Table 2.3. Regression coefficients and coefficient of determination for the model of aspen ring width during the period 1934-1998. 105
Table 2.4. Factor scores and proportion of variation accounted for by each of five principal components. 106
Table 2.5. Multiple regression of aspen ring widths on principal components in Table 2.4. 107
Table 2.6. Regression coefficients and partial coefficient of determination for a model of aspen ring width during the period 1934-1998. 108

Table 3.1. Standardized regression coefficients and coefficient of determination for regional defoliation models. 180
Table 3.2. Regression coefficients and Akaike Information Criterion (AIC) for regional second-order autoregressive (AR(2)) defoliation models. 181

Table 6.1. Shifting disturbances across the provincial grid 1936-1994, revealed by promax-rotated T-mode decomposition. 315
Table 6.2. Environmental correlations for factors derived from unrotated and promax-rotated S-mode decomposition of Cooking. L. municipal grid data 1929-1995. 316
Table 6.3. Environmental correlations for factors derived from unrotated and promax-rotated T-mode decomposition of Cooking. L. municipal grid data 1930-1995. 317
Table 6.4. Spatiotemporal exclusion between pairs of disturbance pulses on the Cooking L. municipal grid 1929-1995, as revealed by promax-rotated T-mode decomposition. 318
Table 6.5. Three patterns of spatiotemporal variability identified by rotated factor analysis that are associated with spatial patterns in forest cover across Cooking L. municipal grid. 319

LIST OF FIGURES

FIGURE .... **PAGE**

Figure 2.1. Location of the study area in central Alberta. 109
Figure 2.2. Location of stands sampled across Cooking L. grid. 110
Figure 2.3. Average June temperature at Edmonton. 111
Figure 2.4. Time-series plots of raw data showing low-frequency variability. 112
Figure 2.5. Clumped distribution of aspen stem ages. 113
Figure 2.6. Age-dependent vulnerability of aspen stems to growth-reduction. 114
Figure 2.7. Spatial correlation between aspen ring widths and FTC cocoon densities. 115
Figure 2.8. Spring precipitation, aspen growth, and FTC cocoon densities 1993-1996. 116
Figure 2.9. Spectra of detrended aspen ring widths, spring precipitation, detrended spruce ring widths 1918-1998. 117
Figure 2.10. Spectral analysis of modeled grid-wide mean aspen ring width chronology. 118
Figure 2.11. Average of unsmoothed spectra for all stand-level aspen chronologies 1934-1998. 119
Figure 2.12. Spatiotemporal autocorrelation in detrended, climate-corrected stand-level aspen ring width chronologies 1934-1998. 120
Figure 2.13. Detrended, uncorrected aspen chronologies from five parts of Cooking L. grid. 121
Figure 2.14. Severe defoliation by FTC in Alberta in 1968 and 1982. 122
Figure 2.15. FTC moths caught in light-traps in Minnesota by Hodson (1977). 123
Figure 2.16. Historical records of FTC in Ontario. 124

Figure 3.1. Weather stations and aspen stands sampled in nine municipalities across northcentral Alberta. 182
Figure 3.2. Mean detrended aspen ring width chronologies for nine municipalities. .. 183
Figure 3.3. Correlation between March-June precipitation at Edmonton and aspen ring width chronologies over Cooking L. grid. 184
Figure 3.4. Correlation between detrended aspen ring widths and kriged estimates of March-June precipitation. 185
Figure 3.5. Cross-spectral coherency between aspen ring widths and kriged precipitation 1908-1998. 186
Figure 3.6. Spectrum of kriged precipitation 1908-1998 at each municipality. 187
Figure 3.7. Average of smoothed spectra for municipal aspen ring width chronologies 1908-1998. 188
Figure 3.8. Spectrum of detrended aspen ring width 1908-1998 for each municipal chronology. 189
Figure 3.9. Annual fluctuation in spatial correlation between aspen ring width and precipitation over nine municipalities. 190
Figure 3.10. Temporal coincidence between aspen ring width and extent of defoliation in

each of nine municipalities. 191
Figure 3.11. Residual aspen ring width from each municipal AR(0) defoliation model. 192
Figure 3.12.Cross-spectral coherence among residual aspen ring widths. 193
Figure 3.13. Residual aspen ring width from Fig. 3.11. averaged over the nine municipalities. 194
Figure 3.14. Aspen ring widths, model fits, and residuals 1908-1998. 195
Figure 3.15. Spectra of aspen ring widths in Fig. 3.14. 196
Figure 3.16. Average spectrum for nine municipal aspen ring width chronologies 1837-1998. 197
Figure 3.17. Spectra of detrended aspen ring widths for three longest chronologies. . . 198
Figure 3.18. Mean aspen ring widths for the three longest boreal chronologies. 199
Figure 3.19. Cross-spectral coherence among climate-corrected aspen chronologies from pairs of neighbouring municipalities. 200
Figure 3.20. Distance-dependent synchrony-decay in aspen growth and kriged estimates of March-June precipitation during 1908-1953 and 1953-1998. 201
Figure 3.21. Uncorrected aspen ring widths for chronologies assembled from clusters of continuously forested and fragmented stands at each of four municipalities. . . 202

Figure 4.1. General location of plots in Minnesota and Saskatchewan. 215
Figure 4.2. Mean aspen ring widths for Kabetogama State Forest and Cloquet Valley State Forest. 216
Figure 4.3. Aspen annual relative growth rates from modern and historical chronologies from two parts of northern Minnesota. 217
Figure 4.4. Aspen annual relative growth rates from modern and historical chronologies from Saskatchewan. 218

Figure 5.1. Autocorrelation and partial autocorrelation functions for municipal aspen ring widths 1908-1994. 244
Figure 5.2. Results from neural net regression. 245
Figure 5.3. Nonlinear stability analysis of neural net regression models. 246
Figure 5.4. Local Lyapunov exponents estimated from 1-unit model for 5-year time-horizon, plotted over time. 247
Figure 5.5. Local Lyapunov exponents and aspen ring widths from Fig, 5.4, averaged over five boreal municipalities. 248
Figure 5.6. Geographic pattern in stochasticity and stability of FTC outbreak models. 249

Figure 6.1. Distance-dependent synchrony-decay among pairs of stand-level aspen chronologies 1936-1994. 320
Figure 6.2. Distance-dependent synchrony-decay among pairs of stand-level aspen chronologies within landscape clusters at two municipalities. 321
Figure 6.3. Comparison, for each municipality, between the spectrum of the mean chronology and the mean of all stand-level spectra. 322
Figure 6.4. Results from *k*-means cluster analysis, mapped in space. 323

Figure 6.5. Mean chronologies from each of nine clusters from cluster analysis. 324
Figure 6.6. Spectra of clustered chronologies. 325
Figure 6.7. Scores for the first nine unrotated factors from T-mode analysis of provincial grid data. 326
Figure 6.8. Loadings for the first nine unrotated factors from T-mode analysis of provincial grid data. 327
Figure 6.9. Spectra of loadings in Fig. 6.8. 328
Figure 6.10. Pairwise plots of unrotated loadings in Fig. 6.8. 329
Figure 6.11. Pairwise plots of promax-rotated loadings in Fig. 6.12. 330
Figure 6.12. Loadings for first nine promax-rotated factors from T-mode analysis of provincial data. 331
Figure 6.13. Scores for first nine promax-rotated factors from T-mode analysis of provincial data. 332
Figure 6.14. Spectra of loadings in Fig. 6.12. 333
Figure 6.15. Temporal scores from unrotated S-mode analysis of aspen chronologies from Cooking L. 334
Figure 6.16. Spatial loadings from unrotated S-mode analysis of aspen chronologies from Cooking L. 335
Figure 6.17. Spectra of temporal scores in Fig. 6.15. 336
Figure 6.18. Pairwise plots of unrotated loadings in Fig. 6.16. 337
Figure 6.19. Pairwise plots of rotated loadings in Fig. 6.21. 338
Figure 6.20. Temporal scores from promax-rotated S-mode analysis of aspen chronologies from Cooking L. 339
Figure 6.21. Spatial loadings from promax-rotated S-mode analysis of aspen chronologies from Cooking L. 340
Figure 6.22. Spectra of temporal scores in Fig. 6.20. 341
Figure 6.23. Temporal loadings from unrotated T-mode analysis of aspen chronologies from Cooking L. 342
Figure 6.24. Spectra of temporal loadings in Fig. 6.23. 343
Figure 6.25. Spatial scores for unrotated T-mode analysis of Cooking L. chronologies. 344
Figure 6.26. Pairwise plots of promax-rotated loadings in Fig. 6.27. 345
Figure 6.27. Temporal loadings from promax-rotated T-mode analysis of Cooking L. chronologies. 346
Figure 6.28. Spatial scores from promax-rotated T-mode analysis of Cooking L. chronologies. 347
Figure 6.29. Mean aspen ring widths across Cooking L. grid. 348
Figure 6.30. Spatial cross-correlation in aspen ring width for pairs of time-averaged growth maps in Fig. 6.29. 349

Figure 7.1. Partial chronologies of aspen ring widths. 367
Figure 7.2. Four examples of mildly non-stationary partial chronologies. 368
Figure 7.3. Temporal factor loadings from unrotated spatiotemporal factor analysis of undetrended aspen ring width chronologies. 369
Figure 7.4. Spatial factor scores from unrotated spatiotemporal factor analysis of

undetrended aspen ring width chronologies. 370
Figure 7.5. Effects of detrending with curves of varying degrees of flexibility. 371
Figure 7.6. Undetrended aspen ring width chronologies averaged over four- to eight-year time-frames. 372
Figure 7.7. Detrended aspen ring width chronologies averaged over four- to eight-year time-frames. 373

Figure 8.1. Aspen stands sampled across the study grid. 412
Figure 8.2. Spatial patterns in winter egg mortality in the shrub and canopy layer, compared to elevation. 413
Figure 8.3. Winter egg morality as a function of elevation and vegetational stratum. . 414
Figure 8.4. Residuals from logistic regression of mortality on elevation, and spatial correlograms. 415
Figure 8.5. Daily minimum temperatures from 1 November 1995 to 30 April 1996. . . 416
Figure 8.6. Winter mortality of canopy-dwelling eggs, winter temperature and average cocoon density 1992-1996. 417
Figure 8.7. Daily minimum urban temperatures from December 1 to March 31 for all winters from 1988-89 to 1995-96. 418
Figure 8.8. AVHRR thermal infrared satellite images of northwestern Canada indicating cloud cover 10-21 January 1996. 419
Figure 8.9. Components of partially density-dependent perturbation effect of winter temperature on egg survival. 420

Figure 9.1. January monthly mean temperature 1913-1985 at six core weather stations in Alberta. 435
Figure 9.2. Coherence in January mean temperature 1913-1985 among all pairs of six weather stations. 436
Figure 9.3. Cross-spectral coherence between January monthly mean temperature and March-June precipitation 1913-1985. 437
Figure 9.4. Results for three scenarios simulated with outbreak model. 438
Figure 9.5. Simulated caterpillar density for the scenario where mean winter egg mortality has been equalized between regions. 439

Figure 10.1. Forest cover across the Cooking L. grid and landscape-dependent spatial variation in parameter a_1. 456
Figure 10.2. Simulation results from two-patch host-parasitoid model showing increasing synchrony for increasing dispersal rate. 457
Figure 10.3. Simulated population density on a 30x30 coupled map lattice. 458
Figure 10.4. The effect of increasing dispersal rate on the scale of clustering, in a homogeneous environment. 459
Figure 10.5. Simulated population density on a heterogeneous 30x30 lattice. 460
Figure 10.6. Simulated population density on a heterogeneous 8x8 lattice. 461
Figure 10.7. Six factors from unrotated S-mode analysis of data in Fig 10.6. 462

LIST OF ABBREVIATIONS

ACF	autocorrelation function
AIC	Aikake information criterion
AR	autoregressive
ARMA	autoregressive-moving average
AVHRR	advanced very high resolution radiometer
CBGR	Cooking Lake-Blackfoot Provincial Wildlife, Recreation and Grazing Area
CVSF	Cloquet Valley State Forest
EINP	Elk Island National Park
ENSO	El Niño-Southern Oscillation
FNN	feed-forward neural net
FTC	forest tent caterpillar
GCV	generalized cross validation
GLE	global Lyapunov exponent
KSF	Kabetogama State Forest
LLE	local Lyapunov exponent
LOWESS	locally weighted smooth scatterplot
LT_{50}	temperature required to kill 50% of a population
MHBS	Ministik Hills Bird Sanctuary
NOAA	National Oceanic and Atmospheric Administration
PACF	partial autocorrelation function
PANP	Prince Albert National Park
PC	principal component
RPCA	rotated principal components analysis
RSM	response surface methodology
TPS	thin plate spline

1. INTRODUCTION

1.1 Background

1.1.1 Animal population cycles and synchrony

Nobody knows why animal populations cycle in synchrony, although there are several general theories (Moran 1953, Bulmer 1976, Anderson & May 1980, Berryman 1981, 1996, Myers 1988, 1998, Barbour 1990, Ginzburg & Taneyhill 1994, Kendall *et. al.* 1999) and system-specific hypotheses (*e.g.* Royama 1992, Sinclair *et. al.* 1993, Myers 2000). The lack of a single, universal explanation for synchronous cycles is perhaps not surprising given the apparent uniqueness of each system.

More remarkable, however, is the disparity in views among ecologists who focus on specific model systems. It is not known, for example, whether synchronized population cycles of Canadian lynx (*Lynx canadensis*) (Elton & Nicholson 1942) are analogous to the chaotic dynamics of a complex deterministic attractor (Schaffer & Kot 1985, King & Schaffer 2001), or if they are more likely a result of the stochastic behaviour of a single-point attractor (Ranta *et. al.* 1997). Similarly, it is not known whether periodic outbreaks of spruce budworm (*Choristoneura fumiferana* Clem.) are due to: (i) multiple-equilibrium dynamics (Southwood & Comins 1976) resulting from the effects of localized predation and weather on mature larvae (Greenbank 1956, 1963, Watt 1963, Morris 1963, Campbell 1993), (ii) cusp-catastrophe dynamics (Murray 1993) of a plant-predator interaction, coupled with dispersal (Greenbank 1957, Ludwig *et. al.* 1978, Clark & Holling 1979, Greenbank *et. al.* 1980), or (iii) moving-equilibrium dynamics of a stochastic metapopulation of interacting host- and parasitoid-guilds (Royama 1992). In each case, the hypothesized mechanisms differ substantially, but evidence for any one view is equivocal.

The slow rate of progress in elucidating the dynamics of such well-studied systems suggests that Kareiva's (1990) "gap between theory and experiments" is rather wide indeed.

Moreover, it is not clear how to close this gap. On one hand, there may be simply a lack of appropriate data to test the theories. On the other hand, the theories themselves may be in need of reformulation. Is it possible that such disparate views on the origin of population cycles are actually compatible with one another? Like the famous dual wave-particle theory of light, perhaps there is a broader pluralistic synthesis that can explain these seemingly incompatible views as manifestations of a single whole. There is a need for progress on both theoretical and empirical fronts.

1.1.2 The forest tent caterpillar

The forest tent caterpillar is a Lepidopteran defoliator of deciduous trees that is found throughout North America (Stehr & Cook 1968). In the northern part of its range, where it feeds primarily on trembling aspen (*Populus tremuloides* Michx.), populations occasionally erupt to very high densities. These can spread, forming large-scale epidemics that eventually collapse with remarkable synchrony (Hildahl & Reeks 1960, Sippell 1962, Ives 1971, Hildahl & Campbell 1975, Hodson 1977, Daniel & Myers 1995).

Like the classic cases of lynx-hare cycles and spruce budworm outbreaks, that of the forest tent caterpillar, *Malacosoma disstria* (Hbn.), is symptomatic of the field of animal population dynamics: there is an abundance of observed patterns, experimental data and speculation, and a paucity of quantitative, testable, and test-worthy predictions.

The pattern of outbreaks is actually quite complex. And though many disparate theories have been proposed to explain the occurrence of outbreaks, none has been so compelling as to quell the debate. A review of the available facts and theories suggests that synthesis is needed. This is the rationale for the current study.

1.1.2.1 Natural history

The natural history and population ecology of forest tent caterpillars in northern regions is well known, and has been summarized before (Hodson 1941, Witter 1979, Ives & Wong 1988, Fitzgerald 1995, Otvos *et. al.* 1998). Life-table studies show that the forest tent caterpillar is attacked by many species of natural enemy, and is vulnerable to mortality by numerous environmental factors (Witter *et. al.* 1972).

Unhatched pharate larvae pass the winter inside their eggs, which are aggregated into bands of 150 to 250 (Witter & Kulman 1969). These are covered by a hygroscopic, foamy substance called spumaline (Hodson & Weinman 1945), which also serves to protect against egg parasitism (Smith & Strom 1993). Egg-bands are typically laid on the tips of twigs in the upper canopy of host-trees (Shepherd & Brown 1971). Although cold-tolerant, eggs are susceptible to freezing by extreme cold (Wetzel *et. al.* 1973, Witter & Kulman 1972). The risk of mortality varies seasonally as a result of changes in egg physiology and fluctuations in temperature (Hanec 1966).

In spring, around the time of aspen bud-break, larvae eclose and feed, if foliage is available. At this early stage, larvae are vulnerable to freezing and starvation (Raske 1975) and entire colonies may be fatally dislodged by windstorms (Blais *et. al.* 1955). Larvae feed colonially for the first four stages, during which time they are subject to predation by spiders, ants, pentatomids, carabids, and birds, and parasitism by several species of Hymenoptera and Diptera (Green & Sullivan 1950, Williams *et. al.* 1996, Parry *et. al.* 1997).

Living gregariously, larvae can contract a nuclear polyhedrosis virus that is often fatal (Stairs 1966). At high densities, they are also vulnerable to microsporidian infections, which reduce larval vigour and adult fecundity (Thomson 1959) and may persist in populations for generations (Wilson 1980). During the fifth larval stage, entire stands of trees can be completely defoliated, and larvae may wander for sizable distances in search of food and/or pupation sites (Batzer *et. al.* 1995). Surviving larvae spin protective silken cocoons in foliage, and pupate.

Typically, a large proportion of larvae are parasitized by tachinid flies. The species *Patelloa pachypyga*, *Leschenaultia exul*, and *Carcelia malacosomae* are especially common (Williams *et. al.* 1996). Many of these parasitoids, upon completing their larval development, drop to the ground and pupate in the litter, where they pass the winter underneath the snow, emerging the following spring. Many tent caterpillar pupae are subject to parasitism by a sarcophagid fly, *Arachnidomyia aldrichi*, which has often been cited as a principal controlling agent.

Around mid-July, two to three weeks after hosts pupate, sexually mature forest tent caterpillar moths emerge, mate, and the females lay eggs. The flight range of moths has not been measured, but adult females are not known to disperse large distances without the aid of unstable air masses (Brown 1965).

1.1.2.2 Outbreak cyclicity and eruptivity

Hodson (1941) remarked that "in spite of the extensive literature on the forest tent caterpillar and evidence of somewhat regular, periodic outbreaks, there have been no critical studies of the progress of outbreaks and controlling factors." Ironically, the number of studies on the forest tent caterpillar has increased exponentially over the last six decades (Fitzgerald 1995) and yet, despite numerous process-oriented and pattern-based studies, the cause of periodic forest tent caterpillar outbreaks remains a mystery. The translation of processes at the organism-level to patterns of population abundance at the landscape-scale has proven to be a difficult problem.

The single, most contentious issue has been whether periodic forest tent caterpillar outbreaks occur by an eruptive or non-eruptive mechanism. This is by no means the central theme of each and every study that has been done, but it is the one common undercurrent theme responsible for the greatest controversy. As such, it serves as a convenient organizing principle for reviewing the available facts and theories.

Eruptive and non-eruptive mechanisms differ in their assumptions regarding the roles played by deterministic and stochastic processes. Non-eruptive hypotheses hold that the density-dependent structure of a predator-prey interaction (*i.e.* geometrical complexity of the deterministic attractor) is rather simple (*e.g.* single-point equilibrium) and that the weak synchronizing effect of correlated random perturbations relies on the action of lagged density-dependent processes. Eruptive hypotheses allow for more complex attractors (*e.g.* exhibiting multiple equilibria and hysteresis effects), and view perturbations as a strong synchronizing force. Through periodic triggering, these perturbations may force the period of oscillation to some value other than the endogenous periodicity dictated by lagged density-dependent processes.

An eruptive hypothesis would conjecture that (1) independently fluctuating populations are occasionally released from regulation about a predation-induced, low-density equilibrium point by the joint action of slow-changing environmental variables (such as forest-structure and plant-quality, which may affect reproductive rates) and fast-changing variables (such as migration or climatic perturbations, which can act as a trigger in the release or collapse of local populations), (2) as a result of migration, outbreaks may spread to new locations, and (3) large-scale climatic perturbations can help to synchronize the release and collapse of populations over large distances. To the extent that predator behaviour and host-plant synchrony are capricious, weather-dependent processes that are difficult to monitor - which seems to be the case with forest tent caterpillar (Parry *et. al.* 1998) - transitions between endemic and epidemic states ought to be difficult to predict.

An eruptive hypothesis of forest tent caterpillar outbreaks has been formally conjectured (Rose 1976, Harmsen *et. al.* 1976, Rose & Harmsen 1978, Rose & Harmsen 1981), and the idea has been considered experimentally (Parry *et. al.* 1997). But, while these studies yielded valuable information, they did not achieve a definitive result. The eruptive hypothesis remains a highly conjectural proposition.

A non-eruptive alternative hypothesis of tent caterpillar outbreaks has not been formulated as precisely, although non-eruptive mechanisms are prevalent in several conceptual models (*e.g.* Ives 1973, Witter *et. al.* 1975, Hodson 1977). As such, the non-eruptive view has not been subjected to rigorous scrutiny.

Berryman (1996) has described a non-eruptive hypothesis of lepidopteran population cycles that synthesizes many elements expressed in these conceptual models of forest tent caterpillar population dynamics. Here, population oscillations are driven primarily by a lagged interaction among sub-populations of caterpillars and specialist predators (*e.g.* parasitoids and virus), which are subject to climatic perturbation, and are prone to synchrony either through dynamic homogenization *via* dispersal (Barbour 1990) or through phase-locking *via* correlated random perturbation (Moran 1953). The idea has been applied most vigorously by Royama (1992), who suggests it is a better alternative than eruptive hypotheses of periodic spruce budworm outbreaks (*e.g.* Morris 1963, Ludwig *et. al.* 1978, Murray 1993).

More recently, non-eruptive mechanistic models similar to Berryman's have been extended into the spatial domain to examine the origins of spatiotemporal patterning in networks of coupled oscillators governed by Ricker-Moran dynamics (Ranta *et. al.* 1998, Kaneko 1998). It is hard to judge how well insights gleaned from coupled-oscillator theory might relate to the dynamics of forest tent caterpillar populations. Dispersal seems to be a key parameter, yet little is known about dispersal behaviour in tent caterpillars and their natural enemies. This has also proven to be a limitation in judging the relevance of eruptive models (Rose 1976).

1.1.2.3 Regionalization of outbreak patterns

The non-eruptive view of forest tent caterpillar outbreak dynamics is supported by the regular periodicity and remarkable synchrony of the four province-wide outbreaks in Ontario which have been mapped at high resolution from 1948 to 1995 (see Daniel & Myers 1995, also Forest Insect and Disease Survey reports 1990-1996). In nearby Minnesota, the pattern of outbreaks has been a little less regular (Hodson 1977) and there has been less enthusiasm for this view (Witter *et. al.* 1975).

In western Canada, there has been little support for the concept of population cycles and population synchrony. Indeed, the lack of synchrony in forest tent caterpillar outbreaks across the Canadian prairies caused Hildahl & Reeks (1960) to reject outright the notion of cyclic outbreaks:

> "The periodicity of outbreaks of the forest tent caterpillar has been recognized by Baird (1917) and other authors, but it is questionable as to how periodicity should be measured. Sippell (1957) expressed periodicity as the period between the first years of outbreak, regardless of whether or

> not the outbreaks were common to specific locations. This method of determining periodicity is satisfactory when individual outbreaks are clearly recognizable, but is not satisfactory under prairie conditions where outbreaks tend to overlap. For this reason it is perhaps advisable to consider periodicity as the time lapse from the first severe infestation at a location to the first infestation of the next outbreak at the same location. Application of this procedure to the records of ten selected locations suggests that periodicity may range from six to 16 years with an average of about 10 years. However these figures do not take into account the fact that four of the locations fell within the paths of outbreaks only once during the 35-year period. There is nothing to indicate outbreaks are cyclic."

In the mixedwood region of Alberta, outbreaks of forest tent caterpillar are thought to be "more frequent and occur over larger areas" than elsewhere in North America (Volney 1988). In characterizing forest tent caterpillar outbreaks in western Alberta, Leech (1944) stated "serious outbreaks of this species often occur at six- to seven-year intervals". Historical defoliation maps from Alberta indicate two major outbreaks from 1957-1962 and 1982-1988 with localized pockets of defoliation scattered through the aspen parkland in the intervening years (Ives 1971, Hiratsuka *et. al.* 1980, 1981, 1982, Hiratsuka & Petty 1982, Moody & Cerezke 1983, 1984, 1985, 1986, Cerezke & Emond 1989, Emond & Cerezke 1989, 1990, Cerezke *et. al.* 1991, Cerezke & Gates 1992, Cerezke & Brandt 1993, Brandt 1994, 1995a, b, Brandt et. al. 1996, Ranasinghe *et. al.* 1997, 1998). Additional qualitative evidence, including a single defoliation map from 1940, suggest there was an earlier large-scale outbreak in the early 1940's (Brown 1941, Leech 1944). Thus, based on limited data, the periodicity of province-wide outbreaks has been approximately 20 years in Alberta.

There is no obvious reason why the degree of forest tent caterpillar outbreak synchrony should differ between Ontario and Alberta. Moreover, there is no good reason why outbreaks in western Canada should occur by an eruptive mechanism while outbreaks in eastern Canada should not. The rule of parsimony suggests that one should seek a simple mechanism for geographic differences in outbreak patterns.

Regional differences in outbreak periodicity might simply be an artifact of differences in sampling effort or detectability bias due to differences in forest cover. For example, Alberta's southern forests are dominated by fragmented stands of pure aspen, whereas Ontario's forests are dominated by continuous, mixed stands. Perhaps outbreaks are less detectable in Alberta owing to a dilution-effect of host-tree abundance on landscape-wide caterpillar density.

Alternatively, a rigorous statistical analysis might reveal that the time-series data are too short to prove conclusively that dynamics differ substantially between provinces. There are only four province-wide outbreaks represented in the Ontario defoliation data, and only two province-wide outbreaks represented in the Alberta data. If outbreaks are caused by highly stochastic population processes, then many more outbreaks might be need to be observed before time-series ensembles could be estimated accurately and differences evaluated for statistical significance. The short length of ecological time-series data appears to be a nearly universal problem in the analysis of oscillatory population dynamics (Turchin 1990, Royama 1992).

In support of the view that outbreak synchrony does not differ substantially between Ontario and Alberta, Sippell (1962) noted that outbreaks are not actually perfectly synchronized in Ontario; they tend to spread rapidly from epicentres in the north toward the east and south, following the direction of prevailing winds. Sippell's data also reveal that the province-wide outbreak from 1930-1945 actually occurred in two spatiotemporally disjoint pulses. [These data, being based on partially anecdotal evidence, were not included in the analysis by Daniel and Myers (1995).] Defoliation maps published by Brown (1938) and descriptive summaries of forest tent caterpillar outbreaks in Ontario (Forest Insect and Disease Survey 1941-1945) show that the first pulse, which affected northwestern and eastern Ontario from 1933 to 1938, lead directly to the second pulse, which affected northeastern Ontario from 1940 to 1945 - implying a lag of five to seven years between pulses. A close look at the progression of the 1949-1956 province-wide outbreak shows qualitatively similar asynchrony between northeastern Ontario and the remainder of the province (Sippell 1962). Here, the second pulse, which affected northeastern Ontario from 1954 to 1956, occurred two to three years after the first pulse, which affected northwestern and eastern Ontario from 1949 to 1953. Thus a single province-wide outbreak lasting many years may actually comprise separate pulses that are slightly lagged in space and/or time.

A similar pattern of spatiotemporally lagged pulse-pairs is reflected in both major outbreaks in Alberta. The first outbreak (1957-1964) started with a pulse that peaked in the southern aspen parkland in 1957, and subsided there while spreading northward to the boreal forest, peaking in 1962. The second outbreak (1979-1989) started with a pulse that peaked in the northern boreal forest in 1982, and subsided there while spreading southward to the aspen parkland, peaking in 1987. Given that an additional fifteen years of data from Ontario (1930-1945) has a large influence on one's impression of provincial outbreak synchrony, it may be that these systems are far too stochastic to infer differences based on only 40-50 years of data.

One problem facing the eruptive hypothesis of outbreak asynchrony is that outbreaks frequently fail to spread across the entire landscape, in both Ontario (Sippell 1962) and Alberta (Ives 1971). For example, if outbreaks are supposed to occur purely by an eruptive mechanism, then it is hard to understand why infestations in central Alberta in 1968-1969 and 1974-1975 failed to develop into province-wide outbreaks, and why the 1960-1970 outbreak in Ontario failed to spread to Thunder Bay and northward along the Missinaibi River valley, as did outbreaks in 1947-1957 and 1973-1983. These observations suggest outbreaks may not spread entirely by means of an eruptive mechanism. Spreading patterns could be an illusion resulting from regional periodicity in population oscillations.

1.1.2.4 Eruptivity and asynchrony

The view that insect outbreak patterns are indicative of outbreak mechanisms has been fostered by Berryman (1981), who sought to categorize common outbreak patterns into functional modes (his Table 4.3). Using his dichotomous key to the classification of insect outbreak patterns, one is led the proposition that forest tent caterpillar outbreaks are "cyclical-eruptive". In the context of classical mechanistic theory, a "cyclical-eruptive" dynamic seems dual, if not paradoxical. And while it is certainly possible to imagine a scenario where (1) outbreaks strictly as a result of some trigger, and (2) this trigger is switched at periodic intervals, this scenario certainly does not fit the known facts of tent caterpillar outbreaks. Cyclical-eruptive duality in insect outbreaks seems especially suspicious because it is the only one of six modal categories for which Berryman (1981) does not provide any examples! Berryman (1987), in an updated version of this classification scheme, suggests that the best example of a cyclical-eruptive insect is the psyllid *Cardiaspina albitextura*.

On the other hand, such duality might be inherent in any large, regionalized system. Indeed, forest tent caterpillar outbreaks may fit into any four of Berryman's (1981) six categories depending on what part of its range is put in focus. They could be classified as either "eruptive" or "gradient" and either "pulse" or "cyclical" merely by shifting the scale and location of analysis. No doubt this is true for many widely distributed, outbreaking insect species.

Asynchronous patterns of spreading outbreaks may be difficult to reconcile using classical models with non-eruptive outbreak mechanism, and they may be relatively easy to reconcile with a classical eruptive model, but they do not necessarily imply eruptivity. Eruptivity may imply asynchrony, but the reverse may not be true because other mechanisms may imply asynchrony as well. Examples include insufficient migratory linkage between two populations with different intrinsic local dynamics, or spatially heterogeneous perturbation regimes. Distinguishing eruptive spread from non-eruptive spread therefore requires high-resolution population data and a valid mechanistic outbreak model - neither of which currently exist in the case of forest tent caterpillar.

A fundamental problem with experimental approaches to testing outbreak eruptivity is that when artificial introductions fail to result in prolonged infestations, it is unclear whether this is because the introduced population was too small to surpass a presumed unstable equilibrium point, or because the hypothetical unstable equilibrium point does not in fact exist. It is also not clear how much of an impact an introduction has to be have before one can infer the existence of a low-density equilibrium. How much of a local population increase is required? How much spread?

Eruptivity is nonetheless a critical hypothesis in need of testing, for major economic decisions and eco-political strategies are based on the premise that populations may exist in either endemic and epidemic states, and that transitions between states might be amenable to manipulation if only the master switches that trigger epidemics and extinctions could be identified. This would imply, for example, that insect outbreaks could be treated in the same effective manner that one fights forest fires, or that endangered species could be saved in the same manner one starts forest fires.

Royama (1992) has devoted much effort to refuting the eruptive hypothesis as it relates to a variety of animal systems, including Canadian lynx, arctic hare, Pacific salmon, azuki bean weevil, and spruce budworm. Some would argue that, despite abundant evidence against the eruptive hypothesis, it is continually buoyed by the ubiquitous and perpetual hope that there are low- and high-density equilibrium points to which populations may be driven, should their high or low number become a concern.

1.1.2.5 Synthetic hypotheses

There is a large volume of quantitative and anecdotal data that any synthetic hypothesis of forest tent caterpillar outbreaks must consider. Because the species' range is large and the spatial variability in temporal dynamics is high, the complex spatiotemporal pattern of forest tent caterpillar outbreaks is difficult to summarize in a few words. Consequently, most studies have focused on only a few of these elements, such as outbreak cyclicity and periodicity.

Researchers have tended to either overlook complexity in observed dynamics, or to narrow the scale of observation such that the observed dynamics are more simple. In the first case, the result is a conceptual theory likely to lack explanatory power (*e.g.*

Sippell 1962, Witter *et. al.* 1975, Hodson 1977, Witter 1979). In the second case, the result is a precise conjecture that is unlikely to be ubiquitously valid (Roland 1993). Both types of hypotheses are useful; however a comprehensive synthesis should embrace the full range of spatiotemporal complexity.

One approach to modeling complexity is to develop a complex theory comprising a long list of *ad hoc* conjectures. The process-model of Rose (1976) demonstrates the value of parsimony in formulating a synthesis: untestable hypotheses, however correct they may be, are scientific dead-ends. Complex *ad hoc* theories can sometimes be reformulated to favour parsimony. However, reformulation in this particular case led to an abstract multiple-equilibrium hypothesis (Harmsen *et. al.* 1976, Rose & Harmsen 1978, Rose & Harmsen 1981) that lacked the authenticity of the original model, and was no more testable.

1.2 Objectives

1.2.1 Overarching problem

This study sought to narrow the gap between theory and data relating to the occurrence of forest tent caterpillar outbreaks. The strategy was to attack the problem from both ends: to collect new data that sheds light on existing theory, and to formulate new theory that explains existing data. The challenge was that, in the case of the forest tent caterpillar, there is no shortage of either explicanda or conjecture. Within this tangled web of fact and fiction lay much potential for synthesis; but the opportunities for misguided interpretation and experimentation were also numerous. The danger was that unstructured, Baconian data-gathering, description and experimentation might obscure more than it clarified.

In short, it was not immediately obvious where one ought to begin in trying to address the overarching problem: are forest tent caterpillar outbreaks eruptive, cyclic, or cyclic-eruptive?

Part of the problem was that none of these possibilities was especially compelling.

Some would say there was roughly equivocal evidence for each. Indeed, the balance of evidence seemed to shift back and forth over the course of the study - even as the literature was being examined and initial data were being acquired.

None of these hypotheses, when phrased this tersely, would have been particularly easy to answer in a short time-frame. Clearly, these broad possibilities need to be distilled into a set of testable conjectures.

1.2.2 Fundamental question

Eruptivity - the tendency for a disturbance in one locality to spread to another by means of autocatalytic local release from some basal equilibrium state - is the single, most fundamental issue addressed by those who study the dynamics of insect outbreaks. But it has proven to be a most elusive question. A more addressable question might be whether forest tent caterpillar outbreaks *necessarily* occur by an eruptive mechanism. For example: perhaps outbreak patterns could be explained by a non-eruptive hypothesis such as the population-cycle hypotheses advanced by Royama (1984) and Berryman (1996). Thus one could ask: is it necessary to accept the eruptive half of Berryman's (1981) "cyclical-eruptive" hypothesis? Is the cyclical component alone *insufficient*?

Royama (1992) argued against the *a priori* use of eruptive models to describe the dynamics of insect outbreaks on the grounds of parsimony, suggesting that: (1) most eruptive process-models are based on theory, rather than on quantitative data demonstrating the existence of an eruptive mechanism; (2) mathematical abstractions of eruptive process-models employ many non-interpretable parameters. Yet Royama's alternative models seem no more parsimonious, for they too required many unjustified assumptions in the form of numerous parameters which, while theoretically measurable, are practically and economically unmeasurable. His azuki bean weevil model, for instance, employs no fewer than 17 parameters, and many of these are tuned by iterative simulation rather than biological experimentation.

It has been counter-argued that it is unfair to place a higher burden of evidence on eruptive modelers. Ludwig *et. al.* (1997), who were instrumental in advancing the multiple-equilibrium theory of spruce budworm outbreaks (Ludwig *et. al.* 1978), argued against Royama's double-standard, stating:

> "The concept of the balance of nature might be taken to imply that the system will maintain its integrity under any sort of perturbation. [...] Our expectation is that things will proceed more or less as before, and that the response of the system will be approximately proportional to the perturbation. Such behavior is shown by the simplest linear models. *Some might argue that a principle of parsimony dictates that such models be used in the absence of strong evidence to the contrary.* The following linear model illustrates the property of global stability, which implies that the system will always return to a certain equilibrium, regardless of how far it is displaced from that equilibrium. A system such as [this] cannot fail us or surprise us. It returns to an equilibrium, no matter how far it is displaced, and the position of the equilibrium changes smoothly with the exogenous variable. Such a system is not suitable for a discussion of possible collapses of natural systems, since such collapses are excluded by assumptions such as [linearity]."

Their point that the simplest linear models cannot surprise us is well taken. However, in instances where we are surprised by the behaviour of an eruptive model, there is a tremendous responsibility to validate that result through rigorous empirical investigation. The problem is that rarely is that challenge pursued (although see Gould *et. al.* (1990) and Parry *et. al.* (1997) for important exceptions), and rarely are those exceptional investigations sufficiently quantitative to lead to a conclusive result.

The fact is that non-eruptive linear models have often surprised us - when they have been subjected to realistic regimes of stochastic perturbation (Moran 1953, May 1973), when they have included multiple trophic interactions (May 1974), when they have been parameterized for chaotic behaviour (May 1976), and when they have been spatially coupled into a lattice (Hassell *et. al.* 1992). Are the eruptivists therefore unnecessarily "assuming the consequences"? Are they mistaking complex dynamics for eruptive dynamics?

The fundamental question of forest tent caterpillar population dynamics thus could be phrased broadly in terms of the necessity and sufficiency of eruptive, cyclic, and stochastic mechanisms in explaining observed spatiotemporal patterns of forest tent caterpillar outbreak.

1.2.3 Principal conjecture

Founded on the conceptual framework of coupled-oscillator theory, as espoused by Royama (1992), the principal conjecture was roughly equivalent to Berryman's (1996) parasitism hypothesis. The specific elements were as follows:

1. Lagged density-dependence of a host-parasitoid interaction leads to a deterministic limit-cycle in abundance of both agents (Nicholson & Bailey 1935).
2. The unstable limit-cycle can be stabilized through more appropriate assumptions about density-dependence (Royama 1992).
3. In the stochastic analog, even when the deterministic component exhibits oscillatory damping, random perturbations can amplify and sustain an oscillation indefinitely (Bulmer 1976, Kaitala *et. al.* 1996, Williams & Liebhold 1995).
4. Small networks of sub-populations that oscillate in this manner can be synchronized, for some subset of parameter space, by three mechanisms: period-forcing by correlated catastrophe (Berryman 1981), frequency-locking by dispersal (Barbour 1990), and phase-locking by low-variance correlated perturbations (Moran 1953).

Several corollary and ancillary elements of practical significance are worthy of explicit mention:

1. Delayed density-dependence might arise from interactions with predators or pathogens, and is not assumed to be solely the result of parasitism, or parasitism by any one species.
2. Regional asynchrony in the timing of catastrophic perturbations can lead to

transient periods of asynchrony in population fluctuations.

3. Perturbations might not act in a vertical manner, pushing a trajectory up or down off the attractor (Royama 1992). Although the perturbations themselves might be density-independent, their effect might be partly density-dependent as a result of density-dependence in either physiological susceptibility to perturbation or demographic vulnerability to perturbation.
4. Although local dynamics are modeled in a spatially implicit manner, it is understood that the logistic formulation of a predator-prey model allows for some spatial structure inherent in the interaction, but simply ignores it. This last corollary anticipates the claim that our hypothesis is so simple that it could never account for fine-scale spatial patterning, which we know from experience occurs in FTC. In fact, this hypothesis is compatible with such patterning; it just can't be used to predict it. Consider: (1) the ability of a temporal predator-prey model to describe the temporal dimension of Huffaker's (1958) spatial experiment with orange mites, and (2) the ability of the spatiotemporal Lotka-Volterra model of Solé & Bascompte (1998) to describe the temporal evolution of the lynx-hare oscillation, while displaying complex patterning in the spatial domain.

According to this model, eruptivity, while perhaps sufficient, was conjectured to be an unnecessary proposition. Cyclicity was conjectured to be necessary but not sufficient. Stochasticity was also conjectured to be necessary but not sufficient. Cyclicity and stochasticity together, when parameterized appropriately, were conjectured to be both necessary and sufficient in explaining the full range of dynamics. This model was taken as the most parsimonious and refutable conjecture that could explain the highly synchronized pattern of forest tent caterpillar outbreaks in Ontario (Daniel & Myers 1995).

In reality, ancillary elements (3) and (4) were not part of the initial working hypothesis. These were added about a year later as a result of (1) growing skepticism about the stochastic simplicity of Royama's (1992) quantitative models and his selective use of data in formulating conceptual models, and (2) growing skepticism about the relevance of small-network models. With regard to the first point, there was a gradual realization that Royama's stochastic concepts might require drastic modification to be applicable to the case of the forest tent caterpillar. For example, outbreak periodicity and phasing might not necessarily be driven by density-dependent deterministic processes; they might be largely a result of stochasticity. With regard to the second point, temporal averaging, selective spatial sub-sampling, and coarse-resolution sampling may hide important spatial and spatiotemporal patterns that might prejudice one's view of population synchrony. As it turned out, the first concern was soon substantiated empirically through a field study. The second concern was substantiated theoretically through spatiotemporal modeling results outlined in the textbook edited by Bascompte & Solé (1998).

A stochastic, cyclic, host-parasitoid hypothesis of tent caterpillar outbreaks is hardly novel, having been discussed in the literature previously (Witter *et. al.* 1975, Hodson 1977). Yet it is worthy of formal consideration because previous attempts at refutation (Daniel & Myers 1995) lacked the necessary analytical sophistication (Roland *et. al.* 1998, Cooke & Roland 2000). Moreover, alternative explanations, which have been unconvincing, due to either a lack of formalization and substantiation (Ives 1973), or parsimony and refutability (Rose & Harmsen 1978), or testability (Harmsen & Rose 1981), have nonetheless persisted in the literature (*e.g.* Parry *et. al.* 1997, 1998). Apparently continual refutation is a worthwhile endeavour.

The principal conjecture, being multi-faceted, was not particularly amenable to a simple experimental approach. The problem is that relating process to pattern requires a quantitative model, and there are too many unknown parameters in the case of the forest tent caterpillar. For example, without knowing the dispersal behaviour, the functional responses, and the stochastic dynamics of each individual species of parasitoid, it is difficult to make the link between the biology and population dynamics of parasitoids and the dynamics of forest tent caterpillar populations. At the same time, no short-term study could amass all this information.

What, then, could be done to best address the fundamental question? Where was the best beginning point?

1.2.3.1 Effect of forest fragmentation and winter climate on outbreak dynamics

Roland (1993) showed that forest fragmentation in Ontario is associated with longer outbreaks of forest tent caterpillar. Roland & Taylor (1995) showed that forest structure influences parasitoid dispersal. Roland & Taylor (1997) showed that spatial patterns of parasitism were related to forest structure and reasoned that this could explain the occurrence of longer outbreaks in fragmented forests. Roland & Kaupp (1995) and Rothman & Roland (1998) showed that other mortality agents could also be influenced by forest fragmentation. Roland *et. al.* (1998) showed: (1) warm winter climate is also associated with longer outbreaks; (2) forest structure has a stronger influence on outbreak duration; (3) forest structure and climate are latitudinally confounded. Cooke & Roland (2000) showed: (1) despite a spatially pseudoreplicated design involving latitudinal confounding in Roland *et. al.* (1998), forest fragmentation is nevertheless associated with prolonged outbreaks; (2) the effects of local forest fragmentation extend into neighbouring townships; and (3) some of the variation in outbreak duration is topographically based.

If forest fragmentation decouples the forest tent caterpillar host-parasitoid interaction, and if winter climatic fluctuations act as a stochastic perturbation on forest tent caterpillar egg survival, then the relationships with outbreak dynamics observed in Ontario should be universal. This seemed to be an important conjecture that was relevant to the fundamental question of how forest tent caterpillar outbreaks occur.

1.3 Methodology

1.3.1 General approach

If outbreaks occur primarily through a stochastic, spatially homogeneous, host-parasitoid interaction, then outbreak patterns at some remote location outside Ontario ought to be fairly predictable given spatiotemporal forest structure and climate data. The wider the range of conditions tested in the remote area, the more robust would be the hypothesis test. A failure to predict outbreak patterns would imply something is missing in the model. An eruptive component might be an obvious candidate.

Alberta was an ideal place to test this prediction because, based on limited data, outbreak patterns there seemed less periodic and less well-synchronized than those in Ontario. Was this difference due to differences in forest structure and climate? And if so, would the relationship stand up to scrutiny when viewed over a long time-frame? Alternatively, were patterns in Alberta more consistent with an eruptive hypothesis? A study in Alberta therefore constituted a strong test of the hypotheses that: (1) outbreak cycles are a result of a stochastic host-parasitoid interaction, and (2) spatial outbreak variability is mediated by variation in climate and forest structure.

Large-scale, high-resolution, long-term population data were needed to test the hypothesis. Even if the results were somehow inconclusive, this descriptive work would constitute a very large piece of explicanda to add to the forest tent caterpillar puzzle. The problem was that aerial-survey data of insect-caused defoliation in Alberta extended back only as far as 1957, suggesting that a dendroecological approach to outbreak reconstruction might be the only hope.

1.3.2 Dendroecological outbreak reconstruction

Swetnam & Lynch (1993) showed that tree-ring analysis can provide continuous, long-term records of past insect outbreaks. Insect defoliation can lead to reduced rates of tree growth (Kulman 1971, Mattson & Addy 1975), and evidence of past defoliation can persist for centuries in the annual rings of their host-trees (Blais 1962, 1965, 1983, Muzika & Liebhold 1999). In the absence of historical population data, tree ring-widths can be used as a proxy measure of herbivory, once the proper adjustments are made for other factors affecting growth. These other factors include: (1) climatic perturbations, such as drought, frost damage to buds, and limb-breakage due to snow; (2) endogenous processes, such as flowering and nutrient sequestration; and (3) local disturbances, such as canopy closure, competitive release, or pathogenic invasion - all of which have lingering effects.

Growth rates of trembling aspen are limited by a multitude of factors that operate at a variety of spatial and temporal scales (Peterson & Peterson 1992). Aspen is generally thought to be limited by moisture availability (Froelich *et. al.* 1956, Duncan & Hodson 1958, Fralish 1972, Hogg 1997), which is determined, regionally, by precipitation in the growing season and, locally, by soil-texture and water-table height (Stoeckeler 1960, Fralish & Loucks 1975, Sucoff 1982). Frosts in late spring are known to kill newly eclosed buds (Rose 1958, Egeberg 1963). These can extend over thousands of square kilometres and can suppress radial growth by as much as 90% for the remainder of the season (Cayford *et. al.* 1959). Limb-breakage from snow accumulating on leaves can occur over large areas during autumn (Gill 1974). This can result in substantial growth-loss, and effects may extend over two seasons if the damage occurs in late spring. Larval populations of several Lepidoptera, notably forest tent caterpillar, large aspen tortrix (*Choristoneura conflictana* [Walker]), and Bruce's spanworm (*Operophtera bruceata* [Hulst]), can attain such high densities that entire stands are completely defoliated (Batzer 1972) and stem-growth is retarded.

Of these factors, the impact of the forest tent caterpillar has been studied most thoroughly (Dils & Day 1950, Rose 1958, Churchill *et. al.* 1964). The frequency, duration, and intensity of these outbreaks is so high that, over the life-span of a tree, defoliation accounts for more variation in aspen growth than does drought (Duncan & Hodson 1958, Hogg 1999). Very rarely - and only under extremely high densities - does the forest tent caterpillar feed on conifers (Nicol *et. al.* 1997). Consequently, during outbreaks, white spruce exhibit no evidence of defoliation (Hildahl & Reeks 1960, Ives 1971), while understorey balsam fir show a positive response to defoliation of overstorey aspen (Duncan & Hodson 1958). Finally, aspen that are defoliated early in the season often produce an annual ring that appears whitish in colour when cross-sections are sanded (Hogg & Schwarz 1999). This is apparently a result of two factors. First, white rings have a disproportionately high number of large vessel elements in the early-wood, and these are whiter than fibrous elements. Second, these elements, in a white ring, appear to be weaker than normal because they are unavoidably ruptured in the sanding process, causing a greater proportion of reflected light to be scattered.

These characteristics make aspen a suitable species for dendroecological reconstruction of forest tent caterpillar outbreaks in Alberta. Although aspen stems in the East generally do not attain 100 years of age, stems twice as old have been found in California, the Rocky Mountains and surrounding foothills (Perala 1991). A systematic spatiotemporal reconstruction of forest tent caterpillar outbreaks has not been attempted previously, although Ghent (1952) used samples from a small area in northern Ontario to confirm a 1937 infestation, and to infer an 1881 infestation. These inferred outbreaks coincided with province-wide outbreaks mapped by Brown (1938) and local outbreaks described by Baird (1917). Consequently, a dendroecological approach was used to reconstruct the history of forest tent caterpillar outbreaks in northcentral Alberta.

Outbreak history is most easily inferred from tree rings when the sampling scheme uses experimental blocking to control for the effects of various factors; however, it is generally difficult to find trees that are known to have been unaffected by past defoliation or drought. Instead, non-host trees are often used as a comparison to control for the effects of defoliation (*e.g.* Swetnam & Lynch 1993). Also, by choosing plots near a weather station, the effect of precipitation on growth can be evaluated - and then removed - using statistically robust techniques (Fritts 1976). However, neither of these methods is perfect. First, non-host trees might respond differently to precipitation than host-trees, and they may be subjected to a different suite of exogenous perturbations, internal processes, and local disturbances (Cook & Kairiukstis 1990). Second, climatic effects are difficult to separate from non-climatic effects if the causative agents vary similarly in time or if they are not functionally independent of one another. Any dendroecological reconstruction of outbreaks must address these challenges.

The concerns are valid in Alberta because growth rates of coniferous non-hosts are regulated exogenously by winter drying (Cayford *et. al.* 1959), and endogenously by masting. Also, weather records are sparse and of short duration. A further problem is illustrated in dendrochronological studies in the western United States, which show effects of: (1) sub-decadal cycles in precipitation associated with the El Niño-Southern Oscillation (ENSO) phenomenon (Stahle *et. al.* 1998, Cook *et. al.* 1999), and (2) bi-decadal drought cycles associated with solar variability (Mitchell *et. al.* 1979, Cook *et. al.* 1997). These specific precipitation patterns are particularly strong in the American west-northcentral region, around Montana (Karl & Koscielny 1982), and probably extend into the Canadian Prairies (Cayan *et. al.* 1998). Finally, Alberta is climatologically heterogeneous (MacIver *et. al.* 1972), such that aspen are more likely to be moisture-limited in the southern parkland than in the northern boreal forest (Hogg 1997).

Through the careful collection, interpretation, and analysis of aspen ring width chronologies it was possible to reconstruct long-term, large-scale, high-resolution patterns of forest tent caterpillar outbreaks in Alberta. The data collected here formed the basis of chapters two, three, four, five, six, and seven. The broad topics covered here were:

(1) causes of recruitment patterns and decadal variability in aspen growth;
(2) dendroecological reconstruction of historical outbreak patterns;
(3) temporal analysis of high-resolution outbreak patterns at small scales;
(4) temporal analysis of low-resolution outbreak patterns at large scales;
(5) effects of forest structure and climate on outbreak synchrony;
(6) spatiotemporal analysis of outbreak patterns at multiple scales;
(7) chaos and local non-linear stability analysis of local outbreak time-series;
(8) the role of various errors and biases in dendroecological interpretation and analysis.

1.3.3 Experimental approach

Populations of forest tent caterpillars in the Edmonton area began collapsing in 1995, when this study was initiated. One field season was spent documenting the stochastic nature of collapse. This led to chapter eight, which covered the following topics:

(1) the complex effect of winter temperature on egg hatch;
(2) the likelihood and importance of partially-density dependent perturbation effects;
(3) the long-term implication of capricious temperature-dependent egg survival.

1.3.4 Synthetic modeling

In order to test the stochastic host-parasitoid outbreak-cycle hypothesis, two approaches were used, and these led to chapters nine and ten. Chapter nine used a stochastic temporal model to try to explain observed asynchronous outbreak cycles in the boreal and aspen parkland regions. It performed poorly. Chapter ten is a first attempt at synthesizing the most pertinent data using a spatiotemporal model. The topics covered here include:

(1) the effect of cyclic winter temperatures on predicted outbreak dynamics;
(2) the role of fragmentation and stochastic perturbation in driving local asynchrony.

1.3.5 Chapter content: executive summary

Chapter 2	Dendrochronology of aspen in the parkland region of Alberta
Chapter 3	Dendrochronology of aspen across central Alberta
Chapter 4	Survivorship bias in dendroecological outbreak reconstruction
Chapter 5	Stability analysis of reconstructed outbreaks of forest tent caterpillar
Chapter 6	Spatiotemporal analysis of forest tent caterpillar outbreak patterns
Chapter 7	The effect of detrending error on pattern detection
Chapter 8	The role of winter temperatures in outbreak collapse
Chapter 9	Induction of outbreak cyclicity through perturbation
Chapter 10	Pattern formation in spatiotemporal host-parasitoid models

1.4 Broad relevance

1.4.1 Global change

In recent decades trembling aspen, *Populus tremuloides* Michx., has become increasingly valuable as a source of industrial wood fibre in western Canada (Bryson 1989, Navratil 1991, Navratil & Chapman 1991, Peterson & Peterson 1992). Although vast, the long-term economic viability of this resource could be threatened if forest tent caterpillar outbreaks become more severe as a result of forest fragmentation (Roland 1993) or climate warming (Fleming & Volney 1995) or both (Roland *et. al.* 1998).

Unfortunately, the effects of weather on the myriad biophysical processes that influence tree and insect phenology, survivorship and population dynamics are poorly understood, and the nature of climate change is uncertain. Through dendroecological outbreak reconstruction using trembling aspen, the current study will help: (1) to understand the influence of climatic variation on outbreak occurrence, (2) to predict the likely impacts on wood production; (3) to manage outbreak populations, should the need arise.

1.4.2 Other systems

The emphasis in the current study is on the stochastic nature of predator-prey interactions in heterogeneous environments. It is expected that a synthetic explanation of forest tent caterpillar outbreaks dynamics may be broadly relevant to other systems as well, especially in those cases where populations live in fragmented habitats and are subject to harsh environmental fluctuations. Development of an empirical hypothesis of forest tent caterpillar outbreak dynamics also may assist in the formulation of new theoretical models that are especially relevant in these situations.

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2. THE EFFECT OF SPRING WEATHER AND INSECT DEFOLIATION ON ASPEN GROWTH IN CENTRAL ALBERTA

2.1 Introduction

In recent decades trembling aspen, *Populus tremuloides* Michx., has become increasingly valuable as a source of industrial wood fibre in western Canada (Bryson 1989, Navratil & Chapman 1991, Peterson & Peterson 1992). Although vast, the long-term economic viability of this resource is threatened by climate warming, which may reduce stem and stand-level productivity *via* increased moisture stress (Zoltai *et. al.* 1991, Hogg 1997), and by outbreaks of the forest tent caterpillar, *Malacosoma disstria* (Hbn.), which have a significant impact on annual growth rates at the stem-level (Dils & Day 1950, Froelich *et. al.* 1955, 1956, Duncan & Hodson 1958, Rose 1958, Churchill *et. al.* 1964, Kulman 1971, Pollard 1972, Hildahl & Campbell 1975, Hodson 1981) and the forest-level (Brandt 1995b).

It is unclear whether reductions in annual growth resulting from outbreaks are currently severe enough in western Canada to warrant protective intervention. Volume-losses could increase if outbreaks worsen as a result of either climate warming (Fleming & Volney 1995) or forest fragmentation (Roland 1993) or both (Roland *et. al.* 1998). Of course, losses from overstorey aspen might be compensated somewhat by gains in understorey aspen, or gains in subsequent years.

The magnitude of risk associated with the double threat of climate change is unknown. Although negative effects of insect defoliation and other stem-level perturbations on aspen growth have been documented, they have not been well quantified (Morgan 1991). More and better impact studies have been called for (*e.g.* Peterson & Peterson 1992); however, for the purposes of long-range wood-supply forecasting, such studies should consider the sensitivity of disturbance processes to changes in climatic parameters. Unfortunately, the effects of weather on the myriad biophysical processes that influence tree and insect phenology, survivorship and population dynamics are poorly understood, and the nature of climate change is uncertain. Thus the critical questions are: (1) what are the weather variables that influence drought and defoliation? (2) which of these parameters are likely to change, and how? (3) what are the likely impacts in terms of wood production?

2.1.1 The critical role of spring weather in northern climates

2.1.1.1 Defoliation by frost and tent caterpillars

Upon the arrival of spring, trembling aspen is among the first tree species to produce leaves, and forest tent caterpillars are among the first insect species to begin feeding on hardwoods (Ives & Wong 1988). Indeed, these organisms may be engaged in a competitive evolutionary race toward increasingly early phenological strategies (Parry *et. al.* 1998). The penalty for early phenology, however, is that anomalously cold weather perturbations in early spring can exact a significant toll on survival. In the colder climates of northern latitudes and high elevations, aspen buds and branches are vulnerable to late frost, hail, and heavy snow loads (Marr 1947, Riley 1953, Cayford *et. al.* 1959, Egeberg 1963, Strain 1966, Gill 1974), while young tent caterpillar larvae are vulnerable to windstorms, freezing, and starvation due to a lack of foliage (Blais *et. al.* 1955, Hanec 1966, Raske 1975).

Cold spring weather is generally thought to have a negative impact on both aspen growth and tent caterpillar survival; however, the effect is not always so simple. The impact of spring weather perturbations for both species depends on the physiological state of the organism, which is a function of its developmental state, which in turn is determined by the cumulative effects of weather in weeks prior to perturbation. For example, the most detrimental effects of a "late" frost in May are observed when prolonged warm weather through late April causes "premature" emergence of aspen foliage or tent caterpillar larvae (*e.g.* Blais *et. al.* 1955). In contrast, cold weather followed by warm weather benefits individuals of both species. Again, it is weather variability over time frames as small as a month that may be most relevant to forecasting regional disturbances that affect the aspen wood supply.

The potential impact of changes in spring climate on forest tent caterpillar outbreaks is uncertain because we lack a basic understanding about the processes underlying forest tent caterpillar population dynamics. First, it is not clear whether a trend toward warmer spring temperatures would favour increased forest tent caterpillar survival or increased vulnerability to cold weather anomalies. Second, if outbreaks are driven by a predator-prey interaction, then the impacts on natural enemies may be just as important. Third, even if the effects of environmental change on organismic survival are simple, the population dynamic consequences may not be so simple (Royama 1992). Without knowing the extent to which periodic outbreaks are attributable to a lagged predator-prey interaction, it is not possible to properly analyze the regulatory role of weather perturbations (Roland *et. al.* 1998).

2.1.1.2 Drought and moisture availability

The aspen parkland is characterized by a moisture deficit (Hogg 1997), so it is not surprising that moisture availability is an important determinant of aspen growth rates in south and central Saskatchewan (Hogg 1999). Moisture availability through the growing season is partially driven by precipitation in spring and early summer. In central Alberta, average monthly precipitation is highest in June, July and August, but it is most variable in April and May (Environment Canada, unpublished data). Thus, in the cold and dry continental climate of northwestern Canada, spring weather should have a strong influence on annual fluctuations in aspen growth rates.

2.1.2 Climatic variability

Alberta's climate is more humid than that of Saskatchewan, and a greater portion of the annual precipitation falls as snow (Canadian Climate Normals, Environment Canada 1990). Therefore the effects of precipitation may differ between these provinces. For example, aspen in Alberta may be less sensitive to variation in precipitation and may be more vulnerable to bud mortality by springtime frost or to crown damage by late spring snows.

The potential for spring snow and frost damage may be higher in Alberta than in other provinces as a result of its unique geographical situation. First, being located in a northerly position, spring weather patterns in Alberta are strongly influenced by cold arctic air masses that move in from the north. Second, being situated nearer the Rocky Mountains than Saskatchewan, Alberta is especially prone to so-called "cold air outbreaks" (Colle & Mass 1995, Hartjenstein & Bleck 1991). Third, southcentral Alberta is more prone to severe winter and spring snow storms that are more typical of the Pacific Northwest. These anomalies occur most commonly when the polar jet stream slips into a southern trajectory on the Pacific coast and flows in a northerly direction over the Rocky Mountains, bringing coastal precipitation meridionally in to central Alberta (Changnon *et. al.* 1993). Fourth, central Alberta is prone to early spring warming as a result of the warm, dry westerly winds, or chinooks, that often blow down from the Rocky Mountains in March and April (Peterson & Peterson 1992). Fifth, the effects of the El Niño-Southern Oscillation are stronger in Alberta than in eastern Canada and they also arrive in the early spring, months before they reach eastern Canada (Shabbar & Khandekar 1996, Shabbar *et. al.* 1997). These sub-decadal fluctuations may enhance climatic variability and thus accentuate the risk of drought or defoliation in Alberta.

Recent advances in North American climatological research have led to increased understanding and predictability of large-scale, low-frequency climatic phenomena such as warming trends (Douglas *et. al.* 1982), decadal drought (Cook *et. al.* 1997, Cayan *et. al.* 1998, Dettinger *et. al.* 1998, Swetnam & Betancourt 1998), the El Niño-Southern Oscillation (Ropelewski & Halpert 1986, Shabbar & Khandekar 1996, Shabbar *et. al.* 1997, Stahle *et. al.* 1998), and meso-scale variability associated with synoptic patterns of atmospheric flow (Karl & Koscielny 1982, Barnston & Livezey 1987) and seasonal precipitation (Changnon *et. al.* 1993, Meko *et. al.* 1993). However, gains here do not necessarily translate to the high-frequency domain of meteorological phenomena measured over smaller spatial and temporal scales. Here, total variation in synoptic parameters may be dominated by anomalous daily events which are localized and highly unpredictable.

2.1.3 Quantifying disturbance impacts

If the incidence of drought and defoliating disturbances depends heavily on weather events occurring in a narrow window in early spring, then there may be severe limits to the predictability of aspen volume losses over static spatial frames as small as 10^4 to 10^6 km^2. Consequently, estimating average long-term expected losses may be a more reasonable objective than predicting precise disturbance schedules. In this regard, gross impact studies would be quite helpful.

The question thus arises: which climatic factors are most important in explaining fluctuations in aspen growth, and how do these effects compare to the effects of defoliation by forest tent caterpillars and other insects? For example, although drought can be severe on the Canadian prairies, defoliation by the forest tent caterpillar is the single largest factor contributing to variation in aspen growth rates in Saskatchewan (Hogg 1999). The primary objective of this chapter is to assess the importance of spring climate and defoliation in determining annual fluctuations in aspen growth in the parkland region of Alberta.

Given that aspen growth may be more limited by forest tent caterpillars than by drought, aspen may be a suitable tree species for the dendroecological reconstruction of historical forest tent caterpillar outbreaks. Reconstructions of western spruce budworm outbreaks using spruce and fir annual ring widths have extended by orders of magnitude the amount of outbreak data available for analysis (Swetnam & Lynch 1993). Thus a secondary objective of this chapter is to determine whether it is possible to correct aspen ring width chronologies for the effects of drought, snowfall, and frost, in order to infer past outbreaks of forest tent caterpillar. Obtaining long-term outbreak data would constitute a first step toward understanding the role of weather and natural enemies in governing outbreak dynamics.

2.2 Methods

2.2.1 Study sites

The study was conducted in central Alberta at the northern limit of the aspen parkland forest region, near Edmonton (Fig. 2.1). The study grid lies in an area that could be classified as a southern outlier of the boreal mixedwood forest (Rowe 1972), although white spruce, *Picea glauca* (Moench) Voss, is not nearly as common as it is in the boreal mixedwood region. The summer climate is also drier than in the boreal region (MacIver *et. al.* 1972, Powell & MacIver 1978). Having an annual moisture deficit, the area is more parkland-like than boreal (Hogg 1997).

The study sites were located on a south-projecting finger of glacial deposit known as the Cooking Lake moraine, which extends along a north-south axis through Elk Island National Park. Sampling was conducted on a partial 10x14 grid of 128 sites that covered 420 km^2 of fragmented aspen forest comprising much of Strathcona county and part of Beaver county (Fig. 2.2). The predominant landform was a knob-and-kettle morainal deposit (Howitt *et. al.* 1988) whose fine-scaled topography provided an opportunity to examine small-scale (10^1 to 10^2 m) responses to precipitation under wet and dry edaphic regimes.

2.2.2 Data collection overview

Estimates of aspen ring widths (1888-1998) and spruce ring widths (1873-1998) were obtained along with estimates of daily mean temperatures and total monthly precipitation from March to September, extreme monthly minimum temperature in May, and total monthly snowfall in May (1886-1998). Also, defoliation by forest tent caterpillar was estimated from published insect surveys for the province of Alberta (1957-1998). Finally, for each stand on the study grid, precise estimates of forest tent caterpillar cocoon density (1993-1998) were made. The specifics of each data element and methods of procurement are described in turn.

2.2.2.1 Tree rings

Aspen trees were felled in each of 128 stands. Several criteria were used in selecting plot locations and sample stems. Only stands of pure aspen, or aspen-balsam poplar, *Populus balsamifera*, were chosen. In each stand, samples were taken from the oldest, healthiest trees that could be safely felled. Trees with obvious crown damage, or numerous fungal fruiting bodies, or discoloured bark were avoided. Trees growing in close competition often had to be ignored for those more easily felled. Also, in many cases landowner preference provided additional constraints. Here sampling was often limited to smaller and less healthy trees.

Three aspen trees were felled in each stand. From each stem, sections were taken up the length of the bole to the base of the crown. As cambial division is initiated at the base of the crown weeks before it is initiated at breast-height (Zimmermann & Brown 1980), it is possible to confirm annual rings missing at breast height by cross-dating with sections from crown-height. This was essential on the local grid because a severe forest tent caterpillar outbreak lasting from 1993 to 1995 was found, in declining stands, to result in occasional years with no growth.

Stem sampling was stratified according to local elevation: the highest site was usually at the top of a crest, or "knob", and the lowest site was usually in a wet depression, or "kettle", near the edge of a slough, where aspen mixed with balsam poplar. The middle site was usually on a slope between the two. Trees were often far enough apart to belong to different clones, although this was not the case in very small stands, which are common in agricultural shelter-belts. Here too, elevational distinctions were less meaningful. The purpose of elevational stratification was to control for within-stand variation in moisture availability, which might mediate tree responses to fluctuations in precipitation (Stoeckeler 1960, Fralish & Loucks 1975, Sucoff 1982).

Basal sections were taken from a total of four large wind-fallen spruce trees located at distant points on the municipal grid. Cores were taken from four additional spruce trees from two additional stands. The reasons for measuring spruce ring widths are twofold. First, spruce growth may be a useful non-climatic predictor of aspen growth because spruce may be more sensitive to precipitation than aspen because spruce in central Alberta are closer to their moisture-driven southern range limit than aspen (Hogg

1997). Second, spruce are not defoliated by forest tent caterpillars. Indeed, they are rarely defoliated at all in this part of Alberta.

All sections were dried at 40°C for several days, and sanded with a table-mounted belt-sander using 15 cm wide 50, 80, and 100 grit belts, and then polished with a palm-sized orbital sander using 150, 220, 320 and 400 grit paper. Annual growth rings were resolved using a 10-60x magnification stereo-microscope with a variety of light sources. Each ring was dated and measured to the nearest 0.01 mm using an ocular micrometer. Sectional chronologies were cross-dated by examining the cross-correlation among ring width profiles, particularly with regard to high-frequency fluctuations in ring width (Pilcher 1990). When high-frequency fluctuations did not correlate well, samples were carefully re-examined for the possible occurrence of a missing ring or a counting error (appendix one).

To estimate annual growth rates, ring widths were measured along a single radial transect across the stem section. The savings in processing time was considered worth the loss in accuracy because it was spatial variation among stands in the temporal autocorrelation structure in ring widths that was important, not the accurate estimation of mean growth rates in each year. Specifically, it was temporal variation in the 0.5 to 0.033 y^{-1} frequency range (2 to 30 y) that was of greatest interest. Any method that compromised the estimation of the autocorrelation structure in this frequency range was counter-productive. Techniques that exacerbated variation in the 0.033 to 0.0066 y^{-1} frequency range (30 to 150 y) were of no concern as these low-frequency cycles and trends would be removed eventually by detrending.

The radius of the pith was measured but not included in calculations of mean chronologies. Similarly, measurements of the first year of secondary growth were also not included for two reasons. First, the boundary between pith and xylem was often difficult to discern, which led to ring width measurement errors. Second, the thickness of the first ring was highly variable as a result of sampling error.

As aspen rings were being measured, they were scored as "white" or "normal". Rings that appear whitish do so because of the disproportionately high number of large vessel elements in the annual ring (Hogg & Schwarz 1999). There are two ways this proportion tends to vary: an increase in the number of layers of large vessels laid down in the early wood, and a reduction in the width of the late wood. Only rings of the first type were scored as white. On rare occasions, when a ring was extremely narrow, intermittent or missing, a check made on a section from the crown would reveal that a ring was present further up the bole; if this ring was white, the lower ring was scored as white. Many rings that appeared whitish with the naked eye did not appear to have the same degree of whiteness or the same cellular structure as others; these were not scored as white. Also many narrow rings appeared whitish merely because they lacked late wood growth; these were not scored as white either, although they frequently occurred the year after a white ring. This scoring policy probably underestimated the incidence of severe defoliation.

Individual ring width chronologies from each tree were detrended to remove non-stationarity due to tree-age effects and local stand effects. Two successive cubic splines with 50% frequency responses of 50 and 25 years (Cook & Kairiukstis 1990) were used to remove the low-frequency variation in growth. These relatively flexible fits were necessary because events such as canopy release and closure may cause sudden shifts in growth rates. Variation in the annual and decadal frequency range was preserved. Most of the pulse-like variation in the bi-decadal range was also retained.

Finally, the detrended stand-wise tree ring width series were averaged over the whole grid to produce a mean chronology suitable for dendroecological interpretation. Some low-frequency variation in ring widths was due to stand effects but was not removed in detrending. The asynchronous portion of this component was minimized by spatially averaging individual tree chronologies. This also served to eliminate asynchronous high-frequency noise and to enhance synchronous high-frequency fluctuations, thus strengthening the common signal in the mid- and high-frequency range.

2.2.2.2 Climate data

2.2.2.2.1 Drought

A single time-series of mean daily temperature and total daily precipitation spanning 1886-1998 was assembled from daily instrumental data for two nearby weather stations: Edmonton City Centre (113.50°W, 53.55°N; 1886-1943), Edmonton Municipal Airport (113.52°W, 53.57°N; 1938-1998), (Environment Canada, Atmospheric Environment Service). Data were available for three other stations that were closer to the study area: Cooking L. Airport (113.13°W, 53.42°N; 1985-1994), Elk Island National Park (112.88°W, 53.60°N; 1967-1988), Edmonton International Airport (113.58°W, 53.30°N; 1959-1998); however, for the purposes of dendroecological reconstruction, homogeneity of temporal variation was considered more important than accuracy. In this regard, all stations showed strong coherence in temporal structure, suggesting little information would be lost in using only the two long-term stations.

Daily precipitation/temperature records were summed/averaged monthly in order to reduce the number of independent variables used in modeling the effect of drought on aspen growth. Initial models of aspen growth indicated that monthly mean temperatures and interactions with monthly precipitation accounted for little variation in aspen growth, suggesting precipitation alone was sufficient for modeling aspen growth.

Annual time-series of monthly precipitation were found to exhibit substantial high frequency variation which resulted naturally from 2- to 3-week periodicity in cyclonic activity. This kind of scaling effect has been termed "framing bias" because it tends to produce negative correlations between neighbouring frames (Royama 1992). As the objective was to explain low-frequency cycles in aspen growth, this high-frequency component of monthly precipitation was viewed as noise. One approach to noise reduction is to use a seasonal frame for summing monthly precipitation in order to "iron out" high frequency fluctuations in precipitation. An anomalously wet or dry seasonal precipitation index would be more indicative of variation resulting from established low-frequency (bi-decadal, decadal, and sub-decadal) atmospheric processes such as solar variability (Cook *et. al.* 1997) and large-scale oceanic effects (Cayan *et. al.* 1999), than from chance realizations of high-frequency atmospheric phenomena.

The period from March 1 to June 30 was found to be an optimal seasonal frame for relating precipitation at Edmonton to aspen growth at Cooking L. The March-June seasonal frame seemed biologically reasonable and is generally supported by the literature (Sucoff 1982, Perala 1991). Consequently instrumental precipitation was summed over that period to produce a spring precipitation index.

2.2.2.2.2 Spring frost

Early May is the approximate time of aspen bud-break. The likelihood of frost damage to developing aspen buds and newly emerged foliage was estimated by using the extreme minimum temperature occurring in the month of May, as no climate data were available regarding the incidence of frost in early May. In reality, the precise date of bud-break varies among seasons, and so, therefore, does the window of vulnerability to frost. Consequently, this overly simplistic statistical procedure ignored the important effect of bud-break phenology on vulnerability to frost.

2.2.2.2.3 Spring snow

A single time-series of snowfall during the month of May was assembled for the period 1881-1998 by choosing the maximum snowfall recorded among nearby weather stations. These stations were the same as those used in assembling the precipitation records. May is sufficiently late in the spring that total monthly snowfall is mostly a result of single snowstorms, not daily accumulations. Thus it is a proximate measure of the amount of snow loading on aspen branches, and the risk of crown damage.

As with frost, the impact of snow depends on leaf phenology. It is the wet snow falling in late May, after leaves have expanded, that is most threatening to aspen crowns. Snow occurring before or around budbreak probably has minimal impact on branch loading. The interactive effect of leaf phenology was not included in statistical analyses.

2.2.2.2.4 Solar variability

A time-series of international sunspot numbers was obtained for the period 1873-

1999 (Sunspot Index Data Centre, Brussels, Belgium).

2.2.2.3 Aerially mapped defoliation

Aerially detected defoliation by the forest tent caterpillar has been mapped in Alberta at moderately high resolution since 1957 (Forest Insect and Disease Survey 1958-1982; Ives 1971, Hiratsuka *et. al.* 1980-1982, Sterner & Davidson 1981-1983, Moody & Cerezke 1983-1986, Kondo & Moody 1987, Cerezke & Emond 1989, Emond & Cerezke 1989, 1990, Cerezke *et. al.* 1991, Cerezke & Gates 1992, Cerezke & Brandt 1993, Brandt 1994, 1995a, b, Brandt *et. al.* 1996, Ranasinghe *et. al.* 1997, 1998). National insect surveys prior to 1939 covered eastern Canada only (de Gryse 1939). From 1940 to 1956 defoliation mapping in western Canada was carried out intermittently (Forest Insect and Disease Survey 1941-1957); however, maps for Alberta were too coarsely resolved for quantitative analysis (*e.g.* Brown 1940, 1941).

Aerial surveys of aspen defoliation are supplemented by a sparse network of ground surveys to confirm defoliator identity. In several years, however, defoliation by large aspen tortrix could not be distinguished from defoliation by forest tent caterpillar because ground surveys were inadequate. This was only a minor problem for the current study because the overwhelming majority of early-season defoliation is caused by forest tent caterpillar (Ives 1981). For example, forest insect surveys did not describe significant populations of large aspen tortrix within the study area. Most of the defoliation by large aspen tortrix in Alberta occurred far outside the grid (*e.g.* Wood Buffalo Park, Red Earth Creek, High River, Keg River, Peace River, Grande Prairie, Hinton, Rocky Mountain House, Calgary, Camrose, Millarville, Stettler, Cypress Hills, Waterton Lakes).

A map of the 128 stands was digitally overlain onto each of the provincial defoliation maps from 1957 to 1998 and the number of stands falling in the zone of severe defoliation was counted. This count was used in calculating the proportion of stands severely defoliated across the grid. Maps were not available for 1978 and 1996 so missing values were estimated by averaging the defoliation values for the years before and after. This seemed reasonable because forest tent caterpillar populations were generally increasing in 1978 (Hiratsuka & Petty 1982) and decreasing in 1996.

2.2.2.4 Caterpillar density and forest cover

Estimates of forest tent caterpillar cocoon density were obtained for each stand over the years 1993-1998. These estimates were derived from counts made over a fairly small collection area (usually less than 0.1 ha). Tree samples covered a wider area and were often taken up to several hundred metres away from the location of cocoon counts in order to avoid damaging these permanent sample plots. The detailed methods of population sampling are described in a related study conducted on the same grid (Roland & Taylor 1997).

Estimates of forest cover, measured as the percent of forest (predominantly aspen) in a square neighbourhood surrounding a stand, were obtained from a classified photo-mosaic of forested and non-forested land (Fig. 2.2a). For the present analysis the size of the neighbourhood was set to 1700m on a side (Fig. 2.2b).

2.2.3 Data analysis

All analyses were conducted with the R statistical package, version 1.0.0 (Ihaka & Gentleman 1996, Hornik 2001).

2.2.3.1 Recent disturbances affecting aspen growth

To determine whether forest tent caterpillars might be responsible for spatial and temporal variation in aspen growth rates, the 1993-1998 caterpillar density data were used to calculate spatial and temporal correlations of density with non-detrended aspen growth rates. Stands were divided into two groups based on the degree of forest cover measured at various spatial scales. Correlations were computed separately for stands located in predominantly continuous forest and stands located in predominantly fragmented forest. With only six years of observations, the relative importance of spring precipitation and forest tent caterpillar density could not be evaluated with multiple regression.

For this analysis non-detrended aspen chronologies were used because trends are difficult to estimate when the later years of a chronology exhibit a temporary reduction in growth. Even stiff cubic splines are flexible enough that temporary suspensions in growth in the latter part of a chronology will be attributed to a terminal downward growth trend. Chronologies ending in 1995 were extremely problematic in this regard because the outbreak had not terminated by then. Chronologies extending past 1996 were less problematic because growth rates generally recovered. Notably, many trees did not recover fully by 1997 or 1998 because they suffered crown damage as a result of the most severe May snow storm of the century, which occurred on 21 May 1997, well after leaves had flushed from buds.

2.2.3.2 Long-term effects of drought at micro-scales

As tree samples were stratified by topographical position, it was possible to determine whether within-stand variation in moisture availability influenced the responsiveness of aspen to precipitation. Paired *t*-tests were used to compare chronologies from upper and lower sites in terms of their variance and correlation with spring precipitation over the period 1938-1998. If moisture was generally limiting, it was expected that, all things being equal, trees from upper sites would be more responsive to variation in precipitation and would show higher variation in growth. Because chronologies based on a single tree are poor estimators of the mean chronology (Cook & Kairiukstis 1990), this analysis was done using three different spatial scales of aggregation: among stands, among blocks, and across the whole grid. Blocks were delineated by partitioning the grid of 128 stands into eight contiguous compartments, each comprising 12-24 stands (Fig. 2.2d).

2.2.3.3 Periodicity in tree ring widths and precipitation

A visual analysis of fluctuations in spring precipitation and tree ring widths suggested that decadal cycles in each were not in phase until the 1920's. Spectral analysis was used to quantify more precisely any periodicity in precipitation and aspen and spruce growth over the period 1934-1998. Cross-spectral analysis was then used to determine the degree of synchrony among pairs of variables. This would indicate, firstly, whether strong correlations among variables were due to strong coherence at low or high frequencies. Secondly, it would indicate whether coherence was strongest in the decadal frequency range. The matter is important because strong decadal coherence between precipitation and aspen ring widths would make it difficult to estimate the independent effects of drought and defoliation incurred by decadal outbreaks of forest tent caterpillar.

2.2.3.4 Stationarity of precipitation responses

Given that Alberta's summer climate has been gradually warming since the beginning of instrumental weather records in the 1880's (Fig. 2.3), non-stationarity of precipitation responses could be a result of increased moisture stress. Consequently the data were split into two series (1873-1933 and 1934-1998) of roughly equal length and aspen growth was modeled as a linear function of spring precipitation and spruce growth in each series. This analysis indicated whether precipitation indices were indeed a stronger predictor of aspen growth in recent times. The breakpoint was set to 1993/1934 (instead of 1935/1936) simply because this coincided with a decadal growth peak when no drought or caterpillar outbreaks were suspected.

2.2.3.5 Possible effects of solar variability

Noting that precipitation exhibited decadal variation reminiscent of the famous decadal solar cycle, the relationship was explored more formally using correlation analysis. Band-pass filtering, which tends to remove variability in frequency ranges lower and higher than some target range, was used to enhance decadal variability in spring precipitation (Guiot 1985). Correlations were then computed between the international sunspot index and both spring precipitation and digitally filtered spring precipitation. This was done for the whole time series as well as separately for the periods 1873-1933 and 1934-1999.

2.2.3.5 Modeling aspen growth

2.2.3.5.1 Effects of spring weather and insect defoliation

Multiple regression was used to determine the relative effects of spring weather and insect defoliation on annual aspen growth over the period 1957-1998. The variables analyzed were: the proportion of stands defoliated, the proportion of stands defoliated in the previous year, the percentage of white rings, precipitation from March through June, the extreme monthly low daily minimum temperature in May, and May snowfall. Spruce ring width was also included as a predictive variable in the analysis because spruce might exhibit drought-related patterns in growth that might not be expressed in a spring precipitation index, but might relate to similar effects in aspen. For example, both spruce and aspen growth might relate to water table height or to summer evapotranspiration rates, which are only partially determined by and indirectly related to spring precipitation. For all analyses white ring counts were $\log_{10}$ transformed.

As some of the dependent variables were inter-correlated due to shared periodicity, a stepwise procedure was used to eliminate correlated dependent variables from the model. A complementary approach was to extract principal components from the original explanatory variables and use these in regression analysis.

2.2.3.6.2 Maximum possible effects of spring weather

Supposing that aspen growth was not actually affected directly by insect defoliation, what was the maximum possible effect that could be attributed to spring weather alone? For the period 1934-1998, where trees seemed more sensitive to precipitation, defoliation variables were removed from the analysis and a multiple regression model was developed using the spring weather indices.

The residuals of this model were taken as a conservative estimate of the temporal variation in aspen growth due to factors other than spring climate. Accordingly, the fitted values, which represented variation in aspen growth due strictly to spring climate, could be used to subtract such effects from stand-wise chronologies. The resulting adjusted chronologies provided a spatiotemporal estimate of variation in aspen growth due to non-climatic disturbance.

2.2.3.7 Disturbance pattern analysis

2.2.3.7.1 Spatiotemporal analysis

The periodicity of disturbance was estimated by spectral analysis (Chatfield 1989). Spatiotemporal synchrony of disturbance was examined with a spatiotemporal autocorrelation function which measured the cross-correlation between maps of aspen growth separated by temporal lags of one to ten years.

2.2.3.7.2 Effect of forest structure

A simple graphical analysis was used to determine if there were any obvious differences in disturbance frequency and severity associated with spatial and temporal differences in forest structure. The grid was partitioned into a northern section (containing Cooking Lake-Blackfoot Provincial Wildlife, Recreation and Grazing Area) and a southern section (including Ministik Hills Bird Sanctuary). Stands in each section were then grouped according to the percentage forest cover in a 1700m square neighbourhood. The resulting partition of five compartments (Fig. 2.2c) was used as a basis for examining detrended aspen ring width chronologies. The specific question was whether forest fragmentation around the bird sanctuary in the 1940's and in the grazing reserve in the mid 1970's led to change in disturbance severity, frequency or synchrony.

2.3 Results

2.3.1 Aspen chronologies

Before presenting results from multivariate regression analysis, it is first instructive to examine the pattern of temporal fluctuations in aspen ring widths in relation to the dependent (*e.g.* climatic) variables. It will become clear that the degree of temporal autocorrelation in each variable and the degree of cross-correlation among variables is sufficiently high that regression results should be viewed with some scepticism.

2.3.1.1 White rings

Of the thousands of annual rings examined, not once did a ring appear whitish because of light coloured latewood; it was always the earlywood or the entire ring that was rich in large vessel elements. Therefore the condition was not caused by any events occurring after the initiation of secondary growth, which is in early June (Dils & Day 1950, Rose 1958). This is fair evidence that white rings not caused by drought, which usually occurs in the hotter and drier months of late summer. They might have been caused by tent caterpillars, which typically begin feeding in May and cause most of their damage in the fifth larval stage, some time in June. Indeed, white rings tended to be especially common during the years 1957-1964, 1986-1989 and 1992-1995 (Fig. 2.4b), when aerial surveys indicated heavy defoliation by forest tent caterpillars (Fig. 2.4a).

Many aspen trees exhibited abnormal rings in the 1997 growing season, when forest tent caterpillar populations were at extremely low levels throughout the study area. These rings were a little narrower than normal, lighter and grayish in colour. They undoubtedly resulted from stem and crown damage caused by the heavy snow that fell on 21 May 1997. Trees that had their stems snapped right in half under the heavy snow load had the whitest and narrowest rings. Here the effect was even stronger in 1998. As these broken stems were likely near death, ring widths for 1997 and 1998 were not included in chronologies for analysis. Trees that were only partially uprooted or whose stems were only partially snapped had whitish rings in 1997, but increased growth rates in 1998. Trees with intact stems had rings that were narrower than normal; however the rings were normal in colour and structure. Rings from all such trees were included in chronologies for analysis.

2.3.1.2 Ring widths

Individual stand-wise chronologies exhibited strong age-related trends and sudden shifts in aspen growth rates. Detrending of these chronologies with cubic splines removed a large portion of low frequency variation, but had minimal effect on variation in the 0.04 to 0.5 y^{-1} (25 to 2 y) frequency range.

Detrended aspen ring width chronologies exhibited approximately 26 disturbances of varying severity and spatial extent over the period 1888-1998. Thirteen of these disturbances were of sufficient extent, intensity and duration that when stand-wise ring width chronologies were spatially averaged across the grid, the resulting mean ring width chronology indicated thirteen multi-year dips of varying amplitude and duration (Fig. 2.4c). Thirteen more were of sufficiently small size, short duration or low intensity that they resulted in only a single-year dip or a shallow multi-year decline in aspen growth.

2.3.1.2.1 Major disturbances

Of the thirteen major, multi-year, grid-wide dips in aspen growth, the latest of these (1993-1995), was undoubtedly caused in part by the forest caterpillar, whose populations were monitored closely throughout the study area over the period 1993-1998. Four more (1957-1960, 1968-1969, 1981-1982, 1987-1988) were also probably caused in part by forest tent caterpillar outbreaks, as they occurred during province-wide peaks in defoliation. Six more (1902-1904, 1914-1917, 1924-1926, 1936-1938, 1949-1950, 1971-1975) might have been due in part to forest tent caterpillar defoliation, as they could be linked to anecdotal evidence from the Edmonton-Slave Lake region (Wolley-Dod 1906, Baird 1917, Tothill 1922, Strickland 1928, Brown 1940, 1941, Ives 1973, Hildahl & Campbell 1975). Two more disturbances (1895-1897, 1941-1943) had strong impacts in certain stands; however no objective evidence could be found substantiating the possibility of localized tent caterpillar infestations in the Edmonton area.

Major episodes of growth depression sometimes coincided with high white ring counts (*e.g.* 1924-1926, 1942, 1957-1960, 1987-1988. 1993-1995); however prominent growth depressions prior to 1924 and during 1936-1938 and 1975-1978 were not associated with high white ring counts (Fig. 2.4b). Similarly, growth depressions during 1949-1950 and 1968-1969 were severe but white ring counts were not exceptionally high.

This suggests that either defoliation by forest tent caterpillars does not always cause white rings or that other factors can cause substantial growth loss without causing white rings.

These thirteen major depressions in aspen growth may not be entirely due to tent caterpillar outbreaks because seven of them occurred in association with decadal minima in spring precipitation (1895, 1937, 1949, 1957, 1968, 1981, 1992) and one occurred during hemi-decadal minima in spring precipitation (1976), while only three occurred during periods of normal or high spring precipitation (1925, 1942, 1987) (Fig. 2.4e). Depressions at 1902-1904 and 1913-1916 were loosely associated with hemi-decadal drought, but spanned at least one year of high precipitation.

The decadal minima in spring precipitation (Fig. 2.4e; clarified in Fig. 2.4f) were notable because they in turn coincided with decadal maxima in the international sunspot index (Fig. 2.4g). In fact, the correlation between the solar index and spring precipitation was higher during the last six solar cycles ® = -0.39; for decadally filtered precipitation *r* = -0.71) than the previous five ® = -0.27; for decadally filtered precipitation, *r* = -0.40). Further, the mean peak solar index was 145.9 for the last six solar cycles (1934-1999) and 78.8 for the previous five solar cycles (1880-1933), suggesting the degree of decadal variability in precipitation may relate to the amplitude of the solar cycle.

2.3.1.2.2 Minor disturbances

Of the thirteen minor disturbances affecting aspen growth, nine (1900, 1907, 1910, 1919, 1933, 1945, 1954, 1964, 1972) occurred in between major disturbance episodes and resulted in mild, but abrupt, grid-wide dips in aspen growth. Three (1922, 1929, 1992) occurred during years closely associated with years of major disturbance, making it difficult to judge whether they occurred independently of drought and tent caterpillar outbreaks. The 1997 minor disturbance was undoubtedly due to crown damage by heavy snow in May.

As with the major disturbances, minor depressions in aspen growth may have been partly due to tent caterpillar outbreaks and partly due to climatic perturbations. From 1892 to 1998 there were nine years when the extreme low daily minimum May temperature dropped below -7°C (1899, 1906, 1907, 1910, 1919, 1924, 1942, 1945, 1954; Fig. 2.4h) and ten years when May snowfall exceeded 18.0 mm (1907, 1918, 1919, 1927, 1928, 1930, 1959, 1987, 1989, 1997; Fig. 2.4i). Comparing years of cold spring weather anomalies to years in which there were minor dips in aspen growth, there was a weak correspondence (Fig. 2.4c, h, i). For example, the only instance where a local peak in aspen growth coincided with a cold weather anomaly was 1928. The only instances where decadal peaks in aspen growth coincided with cold weather anomalies were 1906, 1918, and 1997, and these decadal peaks appear lower than other decadal peaks. These disturbances were sufficiently localized that impacts were not obvious in the mean chronology (growth maps for those years not shown). The 1997-1998 decadal peak likely would have been higher were it not for the impact of the snow that fell on 21 May 1997.

The correspondence between minor disturbances and cold spring weather anomalies was far from perfect, however. First, cold weather anomalies in 1906, 1918, 1928, 1959, and 1989 did not result in abrupt temporary dips in aspen growth (Fig. 2.4c). Second, there was little or no evidence that such dips in 1900, 1933, 1964 and 1972 (Fig. 2.4c) were caused by cold weather anomalies (Fig. 2.4 h, i).

2.3.2 Spruce chronologies

From 1888 to 1998 there were fifteen dry periods where both spruce and aspen growth were lower than average: 1896-1897, 1903-1904, 1913-1916, 1922, 1929-1930, 1936-1938, 1941, 1949-1950, 1957-1958, 1964, 1968-1969, 1976-1978, 1980-1982, 1986-1987, and 1992-1995 (Fig. 2.4d). Although patterns of spruce growth and precipitation sometimes fluctuated synchronously, spring precipitation was better correlated with aspen growth ® = 0.28) than with spruce growth ® = 0.18). In the last 70 years, there has been very little difference in correlations between precipitation and aspen growth ® = 0.48) and precipitation and spruce growth ® = 0.40).

Spruce and aspen ring widths correlated surprisingly well ® = 0.18 and $r = 0.42$ over the periods 1888-1998 and 1928-1998), but would have correlated even better were it not for six sustained dips in aspen growth occurring around 1902, 1914, 1925, 1942, 1960, and 1988. These dips in aspen growth occurred when spruce growth and precipitation were average or above average (Fig. 2.4d, e). Therefore these dips in aspen growth were probably not caused by drought. The most likely cause is defoliation by forest tent caterpillar.

2.3.3 Effect of defoliation on aspen establishment

The overall age-class distribution of sampled aspen stems was hump-shaped, but was skewed toward older age classes as a result of selectively sampling the oldest trees that could be found (Fig. 2.5). In addition to this basic distributional pattern, there were five clumps of cohorts, exemplified by higher than expected counts in the 1918, 1928, 1935, and 1949, and 1962 year classes. Given that a few years may be necessary for a sucker to attain breast-height, this implies that the five cohorts arose during and just after periods where aspen growth was low but spruce growth and precipitation were not low (Fig. 2.4c, d, e). Thus it appears that forest tent caterpillar outbreaks in 1913-1916, 1924-1926, 1936-1938 and 1957-1960 may have helped initiate or promote stand renewal.

The positive effect of defoliation on stand establishment was found to extend several years beyond the recruitment phase. When deviations from mean annual detrended ring widths were summarized on the basis of tree age in a given year and whether or not the grid-wide mean growth rate in that year was above- or below-average, it was clear that, compared to older trees, young trees consistently exhibited smaller reductions in growth in response to disturbance (Fig. 2.6). In fact some young trees actually exhibited positive responses to disturbance (data not shown). In their second and third years after attaining breast-height, trees tended to have wider-than-average rings, and the difference was larger in years of disturbance. In their fourth and fifth years, trees exhibited wider-than-average rings only in years of disturbance. Beyond their sixth year, all trees were equally vulnerable to growth-loss due to disturbance.

2.3.4 Recent disturbance affecting aspen growth

The spatial correlation between forest tent caterpillar cocoon density and ring widths was strong in 1993 and 1994; however it weakened in 1995 and 1996 (Fig. 2.7) as caterpillar populations began to decline to undetectable levels in 1997 and 1998 (Fig. 2.8c). The weak correlation in 1995 might be due to heavy larval mortality, which occurred in June after final defoliation levels had already been determined by early larval feeding in May. The weak correlation in 1996 might be due to the lagged response of aspen to defoliation in 1995. Note growth rates had not yet recovered in several stands, despite having low cocoon densities.

Whether the weak spatial correlation between aspen growth and caterpillar density in 1995 might also be caused by spatially varying impacts of drought could not be directly ascertained, but the possibility exists because 1995 was a very dry year (Fig. 2.8a). Was the temporal pattern of fluctuations in aspen ring widths more closely related to cocoon densities or precipitation? Expecting different responses in forested and agricultural landscapes, the grid was partitioned into two equally sized, semi-contiguous units based on forest cover. Stands with greater than two-thirds forest cover in a 1700m square neighbourhood were deemed continuous; those with less were deemed fragmented (see Fig. 2.2c). Spring precipitation, spatially averaged raw aspen ring widths, and spatially averaged cocoon densities showed clear trends over the period 1993-98 (Fig. 2.8). The temporal correlation between cocoon density and aspen ring width, averaged over the grid, was $r = -0.93$ in the continuous forest and $r = -0.61$ in the fragmented forest. The temporal correlation between precipitation and aspen ring width, averaged over the grid, was $r = 0.87$ in the continuous forest and $r = 0.77$ in the fragmented forest. However, with only six years of data, the first three being dry years of high density and the last three being wet years low density, the analysis was highly pseudoreplicated (Hurlbert 1984). Average caterpillar density correlated significantly with precipitation ® = -0.66), suggesting a multiple regression approach could not be used to tease apart correlations among ring widths, precipitation and caterpillar density.

Notably, it was the lower growth recovery rates in the fragmented forest in 1997 and 1998 that caused the lower temporal correlation between aspen growth and caterpillar density. This was a direct result of damage to tree crowns from the heavy snow that fell on 21 May 1997, and not to any lack of effects from forest tent caterpillar defoliation in years previous. Trees that were phenologically advanced suffered the greatest impact and the spatial pattern of disturbance suggests that trees on warm microclimatic sites were more prone to disturbance. Trees at forest edges accumulated higher snow loads, thus contributing additional fine-scaled variation to the pattern of disturbance.

2.3.5 Long-term effects of drought at micro-scales

A comparison of chronologies from trees on upland and lower elevation sites over the period 1938-1998 showed that the mean variance in growth was higher among trees on upland sites (paired *t*-test, $t = 2.33$, $n = 53$ stands, $p = 0.011$) although annual growth on these sites did not correlate with spring precipitation any better than did annual growth on lower sites ® = 0.26; paired *t*-test, $t = 0.17$, $n = 53$ stands, $p = 0.170$). The 1938 starting date was used in order to optimize the number and length of stand-wise chronologies available for analysis. Results were not sensitive to the particular temporal frame chosen for analysis.

Partitioning the grid into eight blocks (Fig. 2.2d) and aggregating stand-wise chronologies at that scale helped to reduce the noise in the resulting chronologies and increase the overall correlation with local precipitation ® = 0.35), but there was still no difference in correlation between upper and lower sites.

2.3.6 Periodicity in tree ring widths and precipitation

Spectral analysis of precipitation and aspen and spruce growth over the period 1918-1998 indicated a high degree of roughly decadal periodicity in all three variables (Fig. 2.9a-c). Precipitation exhibited a single narrow spectral peak at 0.1 y^{-1} (10 y) while aspen exhibited spectral peaks at both 0.1 and 0.16 y^{-1} (10 y and 6 y) and spruce exhibited a broad spectral peak across this frequency range.

Cross-spectral analysis indicated that coherence between all three pairs of variables was generally high around 0.1 and 0.16 y^{-1} (10 y and 6.2 y), but there were some noteworthy exceptions (Fig. 2.9d-f). Despite the strong decadal periodicity in aspen and precipitation, cross-spectral coherence at 0.1 y^{-1} was not as high between aspen and precipitation (Fig. 2.9d) as it was between spruce and precipitation (Fig. 2.9e). Similarly, cross-spectral coherence between aspen and spruce was not very high at 0.1 y^{-1} (10 y) but was fairly high at 0.16 y^{-1} (6.2 y) (Fig. 2.9f). This suggests there is some decadal disturbance process - such as tent caterpillar outbreak - that affects aspen growth, but does not affect spruce growth and is unrelated to precipitation.

2.3.7 Stationarity of precipitation responses

Multiple regression revealed that aspen ring widths were related to both spring precipitation and spruce ring widths during the period 1934-1998, but not during the earlier period from 1888-1933 (Table 2.1). Whether the data set was split using 1908, 1918, 1928 or 1938 as the pivot year, the results (not shown) were similar. This suggests that drought has become more limiting to growth, possibly as a result of climate warming. It also suggests that regression analysis is an ineffective method for removing the effects of precipitation on aspen growth if temporal observations are assumed to be independent and precipitation responses (*i.e.* regression parameters) are assumed to be stationary.

2.3.8 Aspen growth models

2.3.8.1 Effects of spring weather and insect defoliation

A multiple regression model showed that precipitation and the incidence of white rings were the best predictors of aspen growth over the period 1957-1998 (upper half of Table 2.2). May snow and extreme low temperature in May were not significant. When white ring data and lagged defoliation were not included in the analysis, the significant predictors were spring precipitation and the extent of forest tent caterpillar defoliation (lower half of Table 2.2). Evidently, white ring counts and defoliation data were somewhat redundant, suggesting that white ring counts could be substituted for defoliation data and the analysis extended over the period 1934-1998.

Multiple regression analysis over that period showed that white ring counts, precipitation and spruce ring widths were significantly related to aspen growth (Table 2.3). Principal components analysis of the independent variables showed that precipitation and spruce ring widths loaded fairly heavily onto a first factor and that white ring counts constituted a second factor (Table 2.4). Both factors were significant predictors of aspen growth in a multiple regression analysis (Table 2.5). May snow and May temperature had moderate loadings on factors one and two, respectively, and strong loadings on factors four and three, respectively (Table 2.4). Neither of the two latter factors were significant predictors of aspen growth (Table 2.5).

2.3.8.2 Maximum possible effects of spring weather

When defoliation and white ring data were removed from the initial full model and the regression analysis was conducted over the years 1934-1998, the only variable found to be unrelated to aspen growth was May snow (Table 2.6). The residuals of this model are therefore an estimate of variation in aspen growth due to factors other than spring weather. Because tent caterpillar-related variables were not explicitly included in the model, these residuals offer the best conservative estimate of variation in aspen growth due to forest tent caterpillar defoliation.

A temporal plot of the residuals revealed that low-frequency variability in the original aspen ring width data (Fig. 2.10a) had not been removed (Fig. 2.10b). Spectral analysis indicated that variability in both original and residual aspen ring width was somewhat periodic, with most of the variation occurring in the 0.09 to 0.16 y^{-1} (11.1 to 6.2 y) frequency range (Fig. 2.10d,e).

Inclusion of a first-order autoregressive term in the regression model reduced the amount of decadal variation in residual aspen ring width (Fig. 2.10c) but not to a statistically non-significant level (Fig. 2.10f). This suggests that even if aspen growth occurs by a simple autoregressive process, there is substantial high-order autocorrelation structure that is due to some exogenous autoregressive process - a process such as forest tent caterpillar outbreaks.

2.3.9. Disturbance pattern analysis

2.3.9.1 Adjusting stand-wise chronologies for climatic effects

Aspen ring widths from 1888 to 1933 did not appear to need adjusting for climatic effects. For the period 1934-1998, the fitted values from the climate model presented in Table 2.6 were used to remove the climatic portion of variation from each of the stand-wise aspen chronologies. The single time series of fitted values were subtracted from each of the stand-wise detrended aspen ring width chronologies in order to produce climate-adjusted stand-wise aspen ring width chronologies. The pattern of temporal fluctuations in the resulting mean chronology was therefore the same as in the model residuals. The important effect of removing the temporal climatic variability that is common to all chronologies was to enhance the joint spatiotemporal variability in the adjusted aspen ring width chronologies. By reducing the relative proportion of temporal variation in the data, the relative proportion of spatial and joint spatiotemporal variation increased accordingly.

2.3.9.2 Disturbance periodicity

Spectra of both raw, non-detrended aspen ring widths and detrended, climate-corrected aspen ring widths over the period 1934-1998 showed spectral peaks at 0.11, 0.15, 0.22, 0.26, and 0.34 y^{-1} (9, 6.5, 4.5, 3.8, 2.9 y) (Fig. 2.11). Aside from the obvious lack of variation in detrended chronologies for frequencies lower than 0.08 y^{-1} (12.5 y) - a direct result of detrending - there was little difference between spectra. So while climate-correction reduced the amount of variation in the stand-wise chronologies, the temporal structure was largely preserved: the pattern of fluctuations was still dominated by decadal variation.

The high degree of similarity in spectral properties between the mean spectrum of stand-wise aspen ring width chronologies (Fig. 2.11b) and the spectrum of the mean grid-wide aspen ring width chronology (Fig. 2.10.b) indicated linear scaling of growth disturbances. Decadal disturbances were manifest at both the stand- and grid-level; they were not a large-scale emergent property of aggregated high-frequency fluctuations at the stand-level.

2.3.9.3 Disturbance synchrony

A spatiotemporal autocorrelation function for spatial lag equal to zero showed that disturbance maps three to five years apart tended to be negatively correlated (Fig. 2.12). Where aspen growth reached a minimum on one portion of the grid in a given year, it often peaked in that location four years later. And where aspen growth was not reduced in that year, it often was four years later. Thus while outbreaks were highly synchronized at this small scale of 20x20 km, the semi-localized nature of disturbance led to imperfect disturbance synchrony. For example, there was always at least one stand on the grid exhibiting reduced growth in connection with a pulsing wave of disturbance. That such asynchronous patterns of disturbance can be extracted from tree ring widths proves that dendrochronology is a powerful tool for resolving landscape-dependent disturbance dynamics.

Although disturbances were sufficiently synchronous across the grid to distinguish phases of general rise and decline, they were sufficiently asynchronous at smaller spatial scales that there was some overlap between rising and declining phases. This quasi-periodic/quasi-synchronous/quasi-spreading pattern of disturbance made it difficult to partition the data into temporal slices that clearly separated rising and declining outbreak phases. The occurrence of smaller, localized disturbance pulses made it especially difficult to discern exactly when one outbreak cycle ended and then next began. Thus it was not possible to obtain a good contrast between synchrony of initiation and synchrony of collapse. Indeed, as described by Hildahl & Reeks (1960), it was not even clear that the simple concept of synchronized cycles could be applied. Caveats aside, assuming there were thirteen major outbreak cycles from 1890 to 1998 (Fig. 2.4c), the mean annual standard deviation in ring widths was 0.35 during both rising and declining phases, indicating no difference between synchrony of outbreak and synchrony of collapse.

2.3.9.4 Effects of forest fragmentation

The impact of outbreaks did not appear to worsen either temporally or spatially as a result of forest fragmentation in recent decades (Fig. 2.13). Disturbance synchrony also seemed to be unrelated to spatial differences and temporal changes in forest structure. In the northern part of the grid, the pattern of outbreaks was just as well synchronized between forest types after extensive forest clearing in the 1970's (Fig. 2.13a). And in the southern part of the grid, the pattern of outbreaks was just as well synchronized between forest types after extensive forest clearing in the 1940's and 1950's (Fig. 2.13b).

2.4 Discussion

2.4.1 Aspen chronologies

It has been stated that aspen "wood usually requires special treatment to make the growth rings more obvious" and that aging aspen is "complicated by the occurrence of false growth rings (probably due to insect defoliation)" (Morgan 1991, p. 36); however this was found not to be the case. Perhaps such problems were not encountered in this study because entire cross-sections of aspen were used rather than increment cores. Various deformities in ring patterns were observed and these were likely caused by a variety of natural factors (*e.g.* fire, pathogens, wood-boring beetles). Such deformities, however, did not lead to the sort of errors in aging that might have occurred had only cores been taken.

Very occasionally rings in basal sections were so narrow that individual rings could not be resolved, giving the impression of missing rings. These seem to have occurred during severe outbreaks of forest tent caterpillar. Examination of the corresponding crown sections, however, showed that growth rates in that part of the stem never declined to such low levels. Thus missing rings in basal sections could easily be inferred from the ring patterns in crown sections, and then assigned a width of 0.00 mm.

Many of the aspen annual rings were abnormal in having whitish coloured earlywood. The occurrence of partially white annual rings may explain the belief that insect outbreaks can lead to "false" rings. Examination of these rings under a microscope, however, shows that there is indeed only a single annual ring whose earlywood is dominated by large vessel elements that appear whitish when sanded (see Hogg & Schwarz 1999)..

The pattern of ring widths suggests forest tent caterpillar defoliation is an important factor regulating annual fluctuations aspen stem growth. Yet the proportion of white rings during suspected outbreaks was lower than expected based on reports in Saskatchewan (Hogg & Schwarz 1999). The reason for the discrepancy is unclear but should be addressed. It may simply be that, in this part of Alberta, defoliation does not reach as high a level as quickly in the season. For example, compared to Saskatchewan, peak outbreak densities may be lower or the date of aspen budburst relative to caterpillar egg hatch may be earlier. This would allow a greater proportion of leaves to develop free of herbivory for a longer time.

2.4.1 Effects of spring weather and defoliation

Although there are a number of factors that affect aspen growth, a substantial portion of the temporal variation in aspen ring widths is explained by spring weather anomalies and outbreaks of the forest tent caterpillar. The proportion of variation explained may be as much as 35% or more, depending on the temporal frame of analysis.

Drought had a significant impact on aspen growth and the full effects were surely underestimated. The difference in variance between upland and lowland sites coupled with the significant precipitation-growth correlation suggest moisture was generally limiting, and more so on the upper dry sites. Lower sites were not so wet that aspen responded negatively to precipitation. Weak cross-spectral coherence at 0.1 y^{-1} between aspen/precipitation and aspen/spruce was not due to any lack of decadal variability in either aspen or precipitation, suggesting there is an additional periodic process other than precipitation which regulates aspen growth rates. The most likely explanation is decadal outbreaks of the forest tent caterpillar.

2.4.1.1 Limitations in modeling defoliation impacts

Aerially mapped defoliation was significantly related to aspen growth but it explained little variation. This may be due to technical problems with aerial defoliation mapping and could be compounded by using a statistical model that may not properly reflect the defoliation impact response.

Defoliation is difficult to map accurately from the air. First, if sampling is sparse, one is apt to miss localized pockets of infestation off the flight-line. Second, defoliation boundaries are highly subjective and can be grossly in error under regimes of extensive, but light defoliation. Third, forest connectivity may influence one's concept of outbreak extent, such that mapping biases may not be equal among landscape types. For example, outbreak boundaries might be more difficult to perceive and to map in agricultural landscapes, such as in Strathcona county. Fourth, in sub-epidemic or patchy populations, even the most reliable maps tend to underestimate defoliation at the stand- and tree-level. Thus aerial maps provide a good coarse picture of the extent of severe defoliation, but may be less effective when used in fine-scaled applications.

The regression model used for analysis assumes that the relationship between aerially mapped defoliation and growth impact is linear, however this may be incorrect. If, at the low end of the defoliation impact response function, aspen growth rates are highly sensitive to defoliation, then sub-epidemic populations, which might not be detectable from the air, could have a significant impact on growth. At the high end of the impact response function, if the time at which trees are completely defoliated has a significant influence on growth impacts, then aerial sampling may not be able to resolve such small but crucial differences. For example, if populations are so high that 100% defoliation is attained by the first of June, the impact will likely be more severe than if it is attained by the end of June; yet it is doubtful that aerial sampling in mid-June could resolve such small differences.

Either mechanism might account for the weak correspondence between aerially mapped defoliation and aspen ring widths. For example, substantial defoliation was recorded throughout the aspen parkland in 1968 and 1982; however, none was recorded in the study area (Fig. 2.14) - despite there being substantial aspen growth loss in those and neighbouring years at Cooking L. (Fig. 2.4). Notably, much of the forested area less than 100 km to the West was recorded as having severe defoliation, suggesting that the study area may have been defoliated, but that the defoliation was either not detected or not recorded as severe. Thus several of the dips in aspen ring width chronologies might be due to extensive defoliation by low-density populations or pockets of defoliation by localized infestations, both of which are difficult to detect and map accurately in fragmented landscapes.

2.4.2 Confounding and interaction between spring weather and defoliation

The strong spatial and temporal association between forest tent caterpillar densities and aspen growth from 1993-1998 suggests that aspen growth in the parkland region of Alberta could be strongly limited by defoliation by forest tent caterpillars. It is not possible to say whether reduced aspen growth in 1995 was due to the dry spring of 1995 or the 1995 outbreak of forest tent caterpillars. Both factors may have contributed, either independently or synergistically. The magnitude of these effects and the possibility of interactions can not be estimated with only six years of data.

It is also not possible to say whether the co-occurrence of drought and outbreak in 1995 is mere coincidence. That the same association was observed in 1968 and 1982 (Fig. 2.4) suggests it may not be a coincidence. An association between warm, dry spring weather and forest tent caterpillar outbreaks in Alberta has been noted previously (Ives 1973). Daniel & Myers (1995) claim to have refuted this proposition, but their statistical approach was simplistic in its assumptions (Roland *et. al.* 1998).

Spring weather could influence aspen growth rates indirectly *via* its impact on forest tent caterpillar survival (Ives 1973, 1981). For example, in springtime young larvae are vulnerable to freezing by acute cold (Hanec 1966), chilling by prolonged cold (Raske 1975), and dislodging by windstorms (Blais *et. al.* 1955). Also, mortality by predators or pathogens might be enhanced as a result of slow development during cold weather (Parry *et. al.* 1998) or increased disease transmission rates during wet weather.

These various relationships are poorly understood and so the approach in this chapter is simply to estimate the aggregate effect of spring weather anomalies on aspen growth rates. The matter is important to resolve, however, because spring weather effects may not be additive. This would add yet another level of complexity to the matter of separating effects of drought from those of defoliation. Knowing more about the seasonal biology and population dynamics of forest tent caterpillar, it might be possible to employ a more process-oriented approach to simulating the indirect effects of spring weather on aspen growth.

2.4.3 Dendroecological outbreak reconstruction

A large portion of the variation in aspen ring widths could not be explained. More accurate process-based simulations of aspen responses to drought (*e.g.* Hogg 1999) may help explain some of the temporal variation in mean aspen ring width chronologies. At the same time, much of the unexplained variation may be due to sub-epidemic populations of forest tent caterpillar or defoliation by other lepidopteran aspen-feeders, such as large aspen tortrix (*Choristoneura conflictana* [Walker]), aspen leafroller (*Pseudexentera oregonana*), Bruce's spanworm (*Operophtera bruceata*), or linden looper (*Erannis tiliara*). All of these species can attain high population densities and can reduce aspen growth (Batzer 1972); however, infestations in Alberta tend to be more localized and outbreaks do not last as long as those of forest tent caterpillar (Ives 1981). Also, the forest tent caterpillar is among the earliest to feed on aspen (Ives & Wong 1988), such that it has a larger *per capita* impact than other species. In summary, while it can not be claimed that each and every episode of reduced growth was due to a tent caterpillar infestation, it can be stated with some confidence that the overall temporal pattern of disturbance in the climate-corrected chronologies is broadly indicative of the pattern of forest tent caterpillar outbreaks.

The precise relationship between ring width and insect density is unclear because of the possibility of non-linear responses, physiological preconditioning, impact-sharing among stems, and survivorship bias. Unusually high growth rates immediately after an infestation were a regular feature of stand-wise chronologies. This contributed strongly to the negative correlation between growth maps 3-5 years apart, and may indicate a positive lagged response to stem-wise defoliation or, more likely, a positive response to defoliation in neighbouring stems. High growth rates immediately after an infestation might be a result of increased light and nitrogen availability.

Stem growth is likely to be insensitive to changes in herbivore load above a certain defoliation threshold. That 100% defoliation often occurs at the stand level or larger might suggest the upper end of this non-linear response is often attained during an outbreak. On the other hand, perhaps only those trees suffering severe damage in early summer exhibit maximal responses. As stem-level population density typically follows a clumped distribution, particularly early in the season, only a few stems ought to experience maximal impacts. That severe defoliation rarely caused missing rings suggests this is the case.

The issue of survivorship bias is unresolved but potentially important. Because the trees that are most heavily and continually defoliated are those most likely to die prematurely, a dendrochronological sample from a living aspen forest is biased against detecting past disturbances. Therefore, periods of growth depression early in a mean chronology do not have the same meaning as periods of equally depressed growth later in the chronology: the earlier impacts imply a more severe disturbance. This hypothesis is consistent with the observation that white rings are less prevalent earlier in a chronology. However, knowing that the passage of time influences ring widths in surviving trees is not enough to standardize a chronology: it is necessary to measure this bias precisely. The matter is crucial, because without correcting for survivorship bias, one is invariable led to the conclusion that outbreaks have been worsening. This topic is addressed in chapter four.

Dendroecological reconstruction (*e.g.* Swetnam & Lynch 1993) is less common than dendroclimatological reconstruction (*e.g.* Stahle *et. al.* 1998, Meko *et. al.* 1993) and its methods are less well established. Especially in short-lived species such as aspen, inferring severe disturbance events, such as a tent caterpillar outbreak, is fraught with problems of lagged, scaled, non-linear responses and survivorship bias. Rather than formally reconstructing past caterpillar densities by estimating such effects, the climate-corrected chronologies were taken at face value as being indicative of historical outbreak dynamics. This involves a tacit assumption that defoliation responses were linear and non-lagged and that survivorship bias was negligible. While unrealistic, the alternative has unacceptable risks. It is in many ways preferable to analyze data with known limitations than to speculate at length about reconstructed data whose limitations are unknown.

2.4.4 Outbreak impacts

The clustering of aspen cohorts around non-drought years when growth of dominant trees is low suggests that forest tent caterpillar outbreaks tend to promote stem establishment. Defoliation might cause within-clone shifts in hormonal flows which favour suckering (Navratil 1991). Also, existing suckers may have an opportunity to take advantage of sudden increases in light associated with defoliation (Navratil 1991). Such effects may be enhanced by forest tent caterpillars preferring not to feed in the understorey (Batzer *et. al.* 1995).

The positive growth response of young trees to disturbance implies that volume losses in the canopy were compensated to some degree by gains in the understorey. Such positive responses in the understorey are characteristic of crown-level defoliation by forest tent caterpillars (Froelich *et. al.* 1955) but are not known to occur as a result of drought. Thus defoliation impacts evident in canopy-dwelling stems may not scale up to the whole-stand level. Furthermore, forest-wide projections of growth losses due to insect defoliation (*e.g.* Brandt 1995b) may be biased.

2.4.5 Outbreak patterns

2.4.5.1 Outbreak periodicity

Forest tent caterpillar outbreaks were roughly cyclic with a period of 6.5 to 10 years. The periodicity of oscillations is within the 6 to 16 year range that is commonly cited as the periodicity of outbreaks elsewhere in North America (Hildahl & Reeks 1960, Sippell 1962), but is faster than the mean outbreak periodicity in Ontario, which is roughly 13 years (Daniel & Myers 1995).

The presence of additional higher-frequency components at 0.22 and 0.27 y^{-1} (4.8 and 3.7 y) led to an irregular pattern of large outbreaks being followed by one or more smaller outbreaks. Such behaviour is not easily explained by simple host-parasitoid population models, suggesting outbreaks are not simply the result of stable limit cycles. Population fluctuations in this frequency range have not been reported elsewhere in North America, suggesting that they are either unique to western Canada, or that the aerially mapped defoliation data used in these other studies is insensitive to small changes in population density.

How likely is it that sub-epidemic population cycles occur in reality? The only corroborative evidence comes from Hodson (1977), who showed with moth light trapping data that a 1957 outbreak at Duluth (southeastern Minnesota) coincided with a sub-epidemic population increase at International Falls (260 km NNW of Duluth, in northern Minnesota) and a 1965 outbreak at International Falls coincided with a sub-epidemic population increase at Duluth (Fig. 2.15).

The proximity of Minnesota to Ontario suggests that similar patterns might occur there; however, as in Alberta, there are no data available to test this hypothesis, as mapped defoliation is insufficient to estimate sub-epidemic impacts. A hint of corroboration may lie in Ghent's (1952) analysis of aspen rings from a single stand in Ontario. Not only were there dips in growth in the early 1880's and late 1930's that were associated with forest tent caterpillar outbreaks (Baird 1917, Brown 1938), there were also smaller, sustained dips in 1869-1870, 1889-1890, 1894-1895, 1907-1908, 1911-1912, and 1943-1944 which have not been attributed a cause (Fig. 2.16). These may be due to sub-epidemic populations of forest tent caterpillar.

2.4.5.2 Outbreak synchrony

Fluctuations in aspen ring widths were remarkably synchronous across the grid. Small departures from perfect synchrony were caused by: (1) localization of disturbances over a spatial extent somewhat smaller than the grid and (2) rapidly spreading patterns of disturbance. That growth maps four years apart tend to be negatively correlated provides evidence of disturbance localization (Fig. 2.12). Further evidence of rapid spreading disturbances can be seen in Fig. 2.13, which shows small deviations in the timing of disturbance initiation and arrest, particularly around 1902, 1916, 1925, 1945, and 1960. These effects are obvious when the ring width data are mapped and animated (http://www.biology.ualberta.ca/roland.hp/cooke/anim.html).

Such localized and asynchronous patterns are unlikely to result from a process such as drought, but could easily result from a spreading, self-organized process such as insect outbreak. It is unclear whether transitions between spatial modes of outbreak patterning occur suddenly, say by an eruptive process, or slowly, as a result of poorly synchronized local dynamics. This is an important question from the viewpoint of population management, but unfortunately, these mechanisms are difficult to distinguish by pattern analysis alone. A fundamental problem here is that a partially synchronized network of independent local oscillators can exhibit virtual patterns of spread that are difficult to distinguish from eruptive patterns of spread. Experimentation and process modeling are crucial to gain an understanding in this area.

2.4.5.3 Effects of forest fragmentation and climate change

There were no obvious temporal shifts in outbreak dynamics associated with forest clearing. Fragmentation of forests in the 1940's and 1970's in the west and north parts of the grid also did not cause any obvious change in outbreak dynamics when compared to the temporal dynamics in the continuous forests of Ministik Hills Bird Sanctuary and Cooking Lake-Blackfoot Wildlife, Grazing and Provincial Recreation Area. One can not dismiss the possibility that fragmentation involves neighbourhood effects, whereby impacts are felt in not only the fragmented blocks but also in neighbouring blocks of continuous forest (Cooke & Roland 2000). Such a change would reveal itself not through spatial differences but as a larger-scale change in dynamics over all blocks - an idea that is discussed further in chapter six.

Summer warming seems to have increased the sensitivity of aspen to fluctuations in precipitation. However, there appear to be no changes in outbreak dynamics attributable to climate change. This may simply indicate that ecological and climatic tolerance thresholds have not yet been exceeded. Of course, low frequency variation in outbreak severity, such as a trend toward increasing outbreak severity, would not be detectable with low-frequency detrending methods employed in chronology preparation. The use of cubic splines to remove the effects of tree-age and stand dynamics would inadvertently remove any such trends.

2.5 Conclusion

Aspen growth in the parkland region of Alberta is determined by both spring weather and defoliation by forest tent caterpillars. The incidence of spring frost may contribute significantly to growth reduction, while spring snowstorms contribute little to the overall pattern of variation in growth. Most of the explained variation in aspen growth is attributable to drought and defoliation; however it is unclear which of these is more important because, since the 1920's, decadal outbreak cycles have been well synchronized with decadal precipitation cycles. Similar studies conducted in areas less prone to drought, should help clarify this issue. One problem with extending the range of study, however, is that more care must be taken to control for the effects of defoliation by species other than the forest tent caterpillar. Chapter three describes similar studies in the boreal forest to the north.

A substantial portion of the temporal variation in aspen growth is unexplained by either spring weather or defoliation. Much of this variation may be attributed to joint spatiotemporal variation caused by the nucleation, spread, and heterogeneous collapse of insect outbreaks. This possibility is investigated in chapter six.

It appears that aspen in the parkland region of Alberta are indeed limited by moisture availability and that climate warming could result in reduced growth rates. Aspen growth is also limited by forest tent caterpillar populations. But until more is understood about the relationship between weather and outbreaks of the forest tent caterpillar, no predictions can be made regarding the likely impacts under climate change scenarios. Some progress on this topic is made in chapters eight and nine.

There are minor episodes of depressed aspen growth that are not due to drought but may be due to defoliation by populations of insects that escape detection by aerial defoliation mapping. Irregular, aperiodic population cycles are difficult to reconcile with classical views of forest insect population dynamics, suggesting that something is missing in our basic understanding about the deterministic processes governing population fluctuations. Attempts to explain this puzzle are presented in chapters five and nine.

The dynamics of forest tent caterpillar outbreaks have changed only a little despite large-scale climate warming and severe forest fragmentation. Replication of this study in other locations might help substantiate this result. This idea is left for future research.

If impacts during future outbreak cycles exceed economic tolerance thresholds, protective action may be desirable. However our current understanding of forest tent caterpillar population dynamics is insufficient to prescribe credible population management strategies. Specifically, it is unclear what effect forest protection by insecticidal spraying would have on the balance between forest tent caterpillars and their natural enemies. The fundamental problem is that it is not known how delicate this balance is. Forest management plans, in order to have long-term economic viability, must be based on sound ecological reasoning. This is a major challenge when dealing with such powerful and dynamic forces as drought and insect outbreaks.

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Table 2.1. Regression coefficients and partial coefficient of determination for aspen ring width modeled as a function of spring precipitation and spruce ring width in two time periods.

period	term	estimate	standard error	significance	R^2
1888-1933	precipitation	-0.000493	0.000692	0.480	
	spruce	0.0367	0.131	0.780	
	model			0.746	-0.032
1934-1998	precipitation	0.00136	0.000459	0.004	
	spruce	0.426	0.188	0.027	
	model			< 0.001	0.257

Table 2.2. Regression coefficients and coefficient of determination for the full, partial, and step-wise reduced models of aspen ring width during the period 1957-1998.

model	term	estimate	standard error	significance	R^2
full	defoliation	0.0006028	0.0012528	0.637	
	lagged defol.	-0.0006816	0.0010952	0.538	
	white rings	-0.2188602	0.0892946	0.020	
	precipitation	0.0015893	0.0006686	0.023	
	spruce	0.3687536	0.2570980	0.161	
	temperature	0.0050052	0.0139163	0.721	
	snow	-0.0016463	0.0047512	0.731	
	model			0.004	0.327
reduced	white rings	-0.2265603	0.0582550	< 0.001	
	precipitation	0.0020347	0.0005252	< 0.001	
	model			< 0.001	0.386
partial	defoliation	-0.0017375	0.0009676	0.0809	
	precipitation	0.0014529	0.0006797	0.0394	
	spruce	0.2689773	0.2765685	0.3373	
	temperature	0.0046236	0.0150739	0.7608	
	snow	-0.0045338	0.0048801	0.3591	
	model			0.0133	0.225
reduced	defoliation	-0.0020750	0.0008784	0.0232	
	precipitation	0.0017231	0.0005796	0.0050	
	model			0.0012	0.254

Table 2.3. Regression coefficients and coefficient of determination for the model of aspen ring width during the period 1934-1998.

term	estimate	standard error	significance	R^2
white rings	-0.2094031	0.0494584	<0.001	
precipitation	0.0013882	0.0003988	0.001	
spruce	0.4462414	0.1692177	0.011	
temperature	0.0101317	0.0074687	0.180	
snow	-0.0016874	0.0035400	0.635	
model			<0.001	0.443

Table 2.4. Factor scores and proportion of variation accounted for by each of five principal components.

Variable	PC1	PC2	PC3	PC4	PC5
white rings	-0.192	-0.699	0.308	0.571	-0.231
spruce	-0.625	0.277	-0.146	-0.081	-0.710
precipitation	-0.555	0.377	0.062	0.471	0.569
temperature	0.222	0.430	0.848	0.059	-0.209
snow	-0.463	-0.329	0.401	-0.665	0.273
prop. var.	0.320	0.235	0.189	0.154	0.103
cum. var.	0.320	0.555	0.744	0.897	1.000

Table 2.5. Multiple regression of aspen ring widths on principal components in Table 2.4.

term	significance	R^2
PC1	0.001	
PC2	<0.001	
PC3	0.660	
PC4	0.718	
PC5	0.704	
model	<0.001	0.443

Table 2.6. Regression coefficients and partial coefficient of determination for a model of aspen ring width during the period 1934-1998. The effect of forest tent caterpillars, as measured by defoliation and white ring counts, was not included in the model.

term	Regression			
	estimate	standard error	significance	R^2
spruce	0.5199024	0.1905897	0.008	
precipitation	0.0013247	0.0004512	0.005	
temperature	0.0140774	0.0083907	0.099	
snow	-0.0049036	0.0039150	0.215	
model			< 0.001	0.286

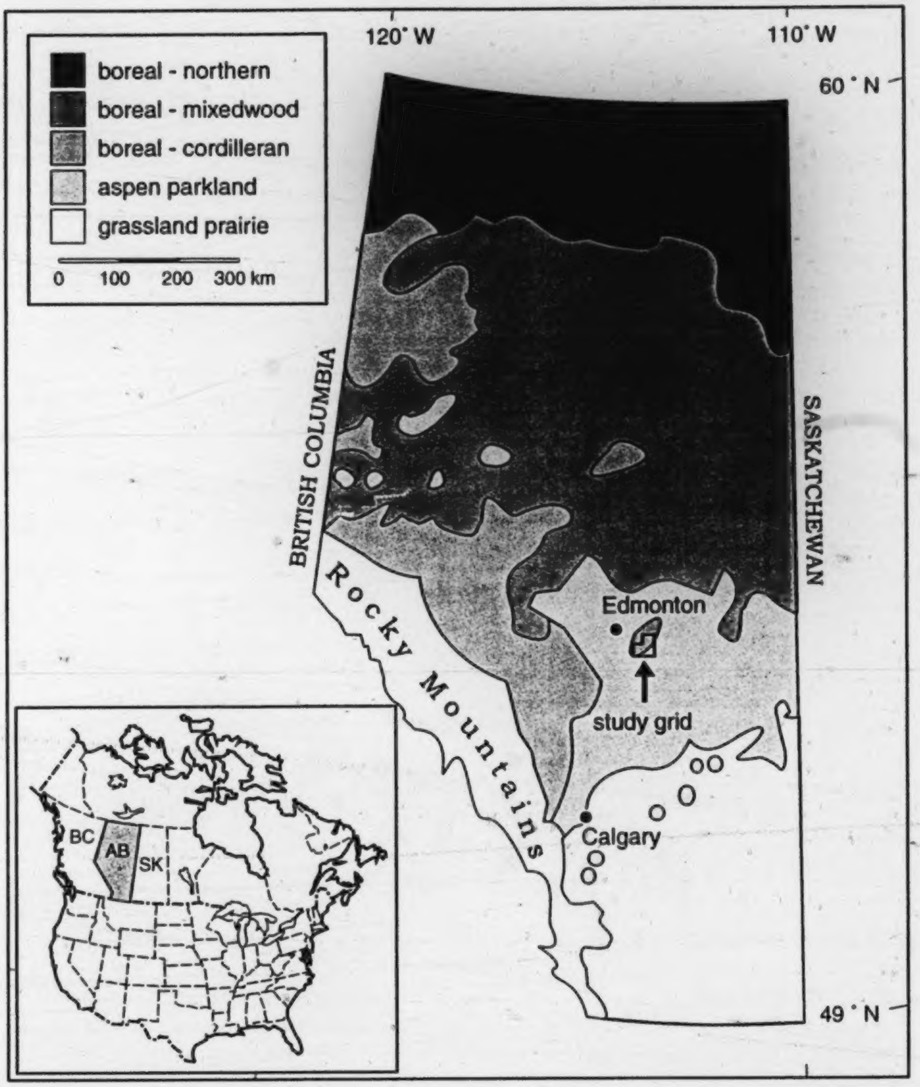
boreal - northern
boreal - mixedwood
boreal - cordilleran
aspen parkland
grassland prairie
0 100 200 300 km
120° W
110° W
60 ° N
49 ° N
BRITISH COLUMBIA
SASKATCHEWAN
Rocky Mountains
Edmonton
study grid
Calgary
BC
AB
SK

Figure 2.1. Location of the study area in central Alberta. Major forest regions redrawn from "Forest Regions of Canada" (Canadian Ministry of Supply and Services 1992, ISBN 0-662-97746-7). Boundaries for cordilleran, mixedwood, and northern sub-regions of the boreal forest redrawn from Rowe (1972).

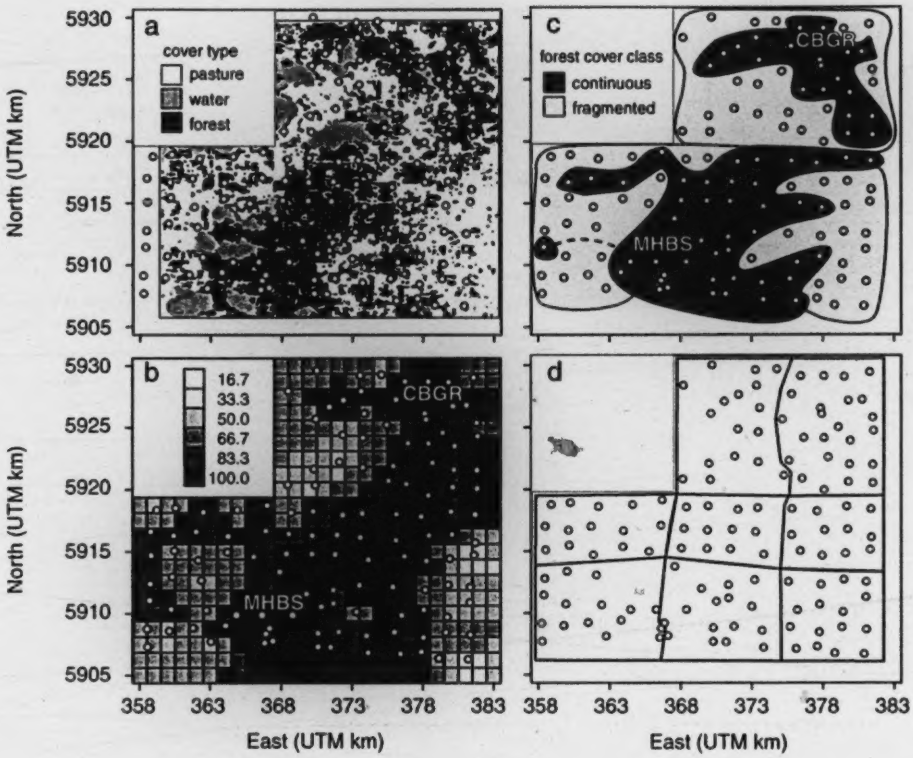
a
cover type
pasture
water
forest
b
16.7
33.3
50.0
66.7
83.3
100.0
CBGR
MHBS
c
forest cover class
continuous
fragmented
CBGR
MHBS
d
North (UTM km)
5930
5925
5920
5915
5910
5905
358
363
368
373
378
383
East (UTM km)

Figure 2.2. Location of stands sampled across Strathcona and Beaver counties and partitions used in summarizing aspen ring width chronologies. Stand locations shown as white circles. Symbols MHBS and CBGR denote Ministik Hills Bird Sanctuary and Cooking Lake-Blackfoot Wildlife, Grazing and Provincial Recreation Area. (a) classified air photo showing land cover types; (b) percent forest cover in 1700 x 1700m blocks around plot centres; (c) a partition of five compartments based on latitude and forest cover; (d) an arbitrary partition of eight compartments.

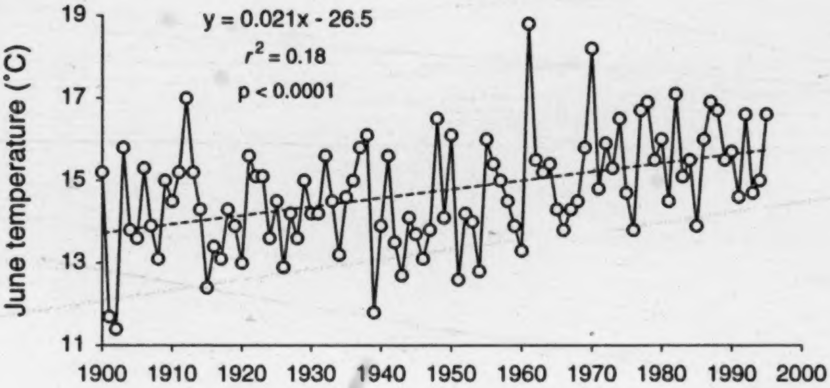

Figure 2.3. Average June temperature at Edmonton (Environment Canada, Atmospheric Environment Service).

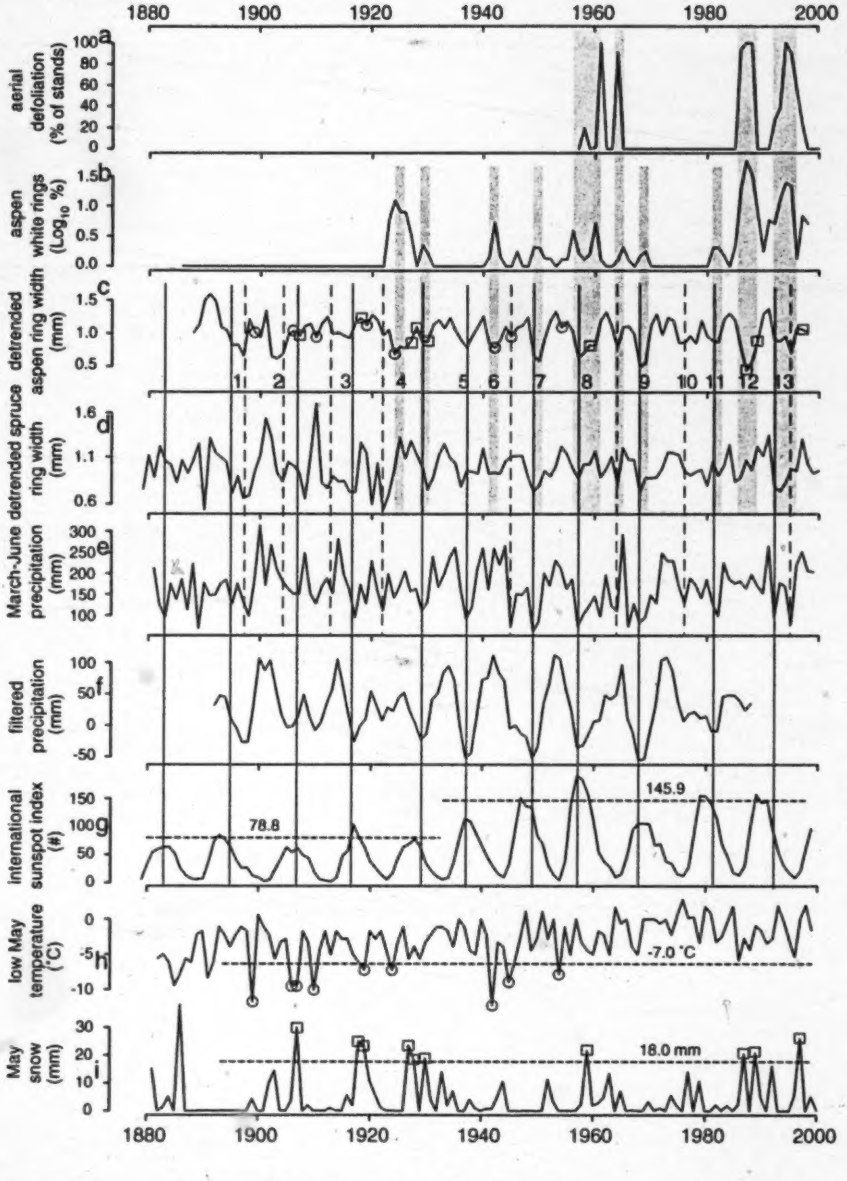

Figure 2.4. Time-series plots showing substantial low-frequency variability in all data. Circles and squares indicate springs with cold temperature and heavy snow, respectively. Suspected forest tent caterpillar outbreak cycles in (c) are numbered from 1 to 13.

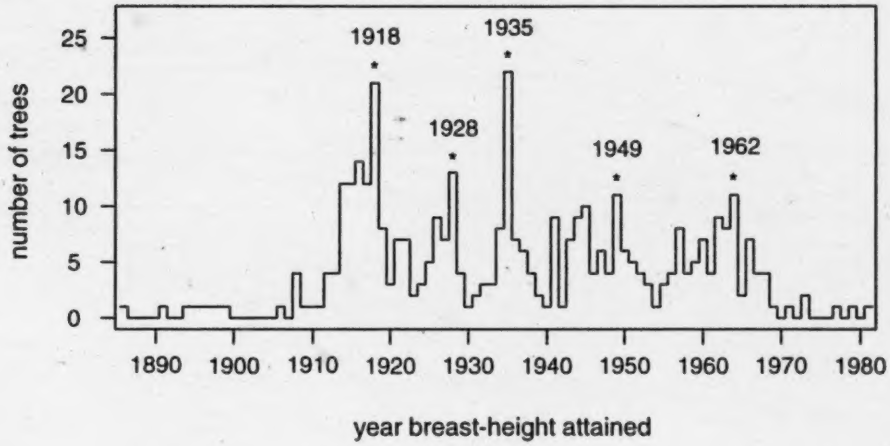

Figure 2.5. Clumped distribution of aspen stem ages caused by decadal pulses of recruitment associated with outbreaks of forest tent caterpillar. Asterisks denote years of peak recruitment into the 1-2 m height class.

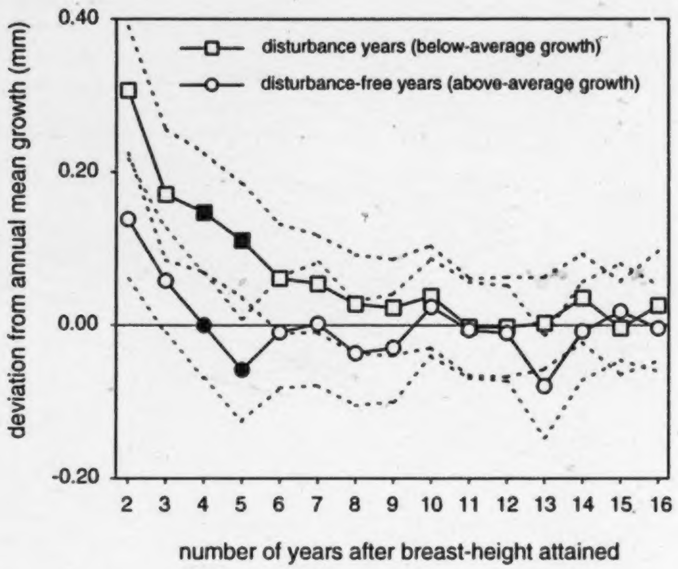

Figure 2.6. Age-dependent vulnerabilty of aspen stems to growth reduction by disturbance. In years with no disturbance, the youngest trees (those that have attained a height of 1-2 m for fewer than four years) exhibit growth rates that are higher than average (positive deviation). In years with disturbance, the size of the deviation is larger and the effect extends out to include trees that have attained a height of 1-2 m for four or five years.. The difference shows that young trees are less vulnerable to disturbance than are older trees. Shaded symbols indicate significant differences between age-dependent growth deviations in years with and without disturbance. Dashed curves indicate 95% confidence intervals on growth deviations.

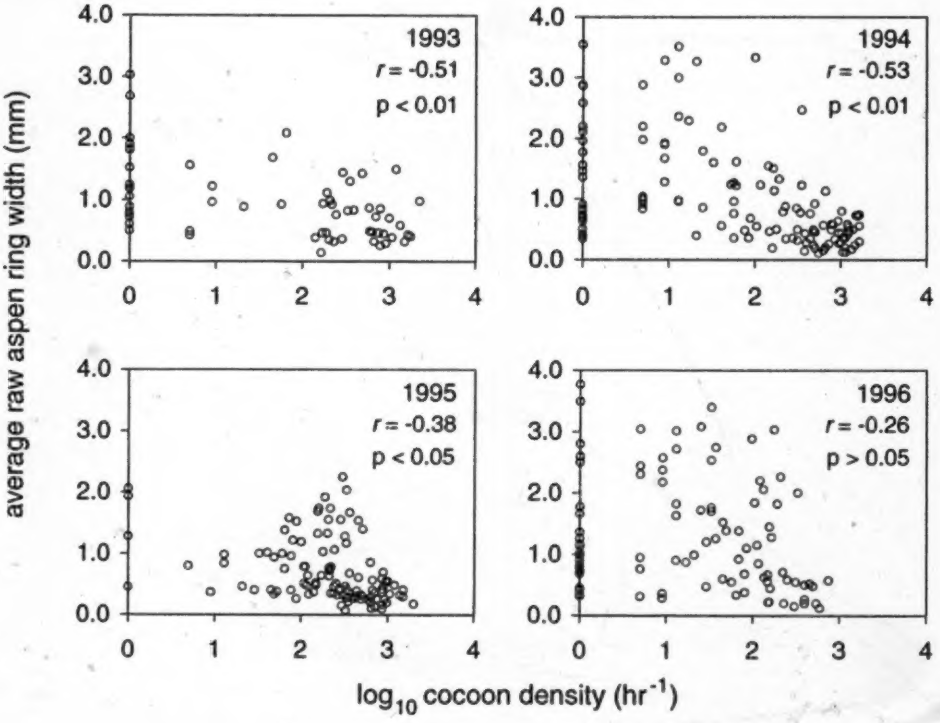

Figure 2.7. Spatial correlation between aspen ring widths and forest tent caterpillar cocoon densities for each year 1993-1996 on the study grid.

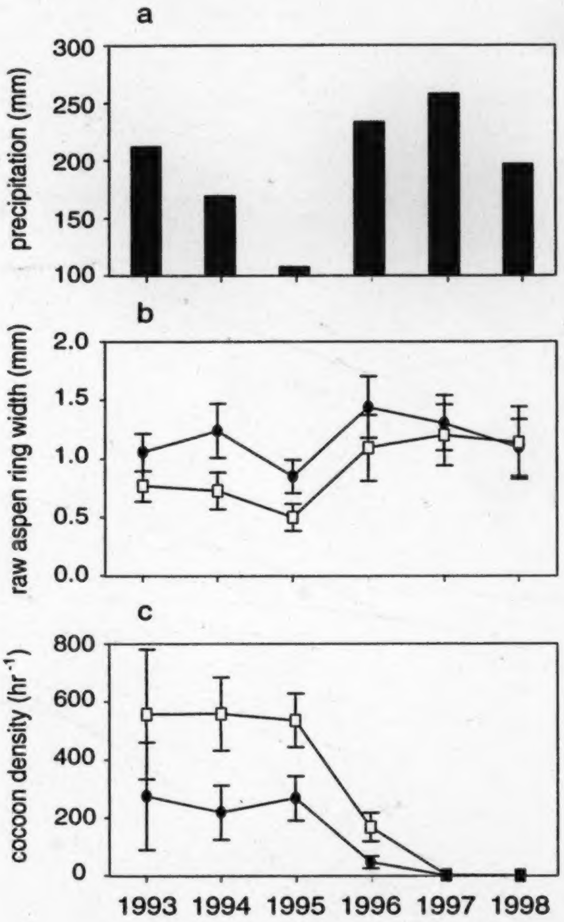

Figure 2.8. Spring precipitation (a), aspen growth (b), and forest tent caterpillar cocoon density (c) over the period 1993-98 on the study grid. Precipitation is for March through June at Edmonton International Airport. Aspen ring widths and cocoon densities are spatial averages for all continuously forested (open squares, n = 60) and fragmented (closed circles, n = 63) plots. Error bars indicate 95% confidence intervals.

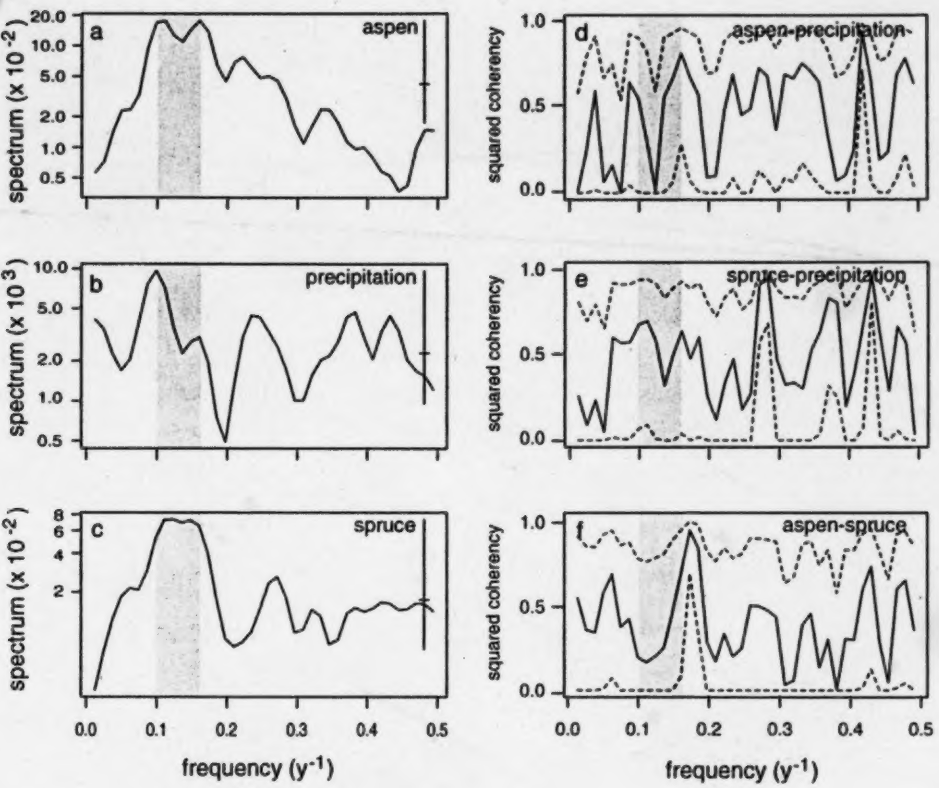

Figure 2.9. Spectra of: (a) detrended aspen ring widths; (b) spring precipitation; (c) detrended spruce ring widths, over the period 1918-1998, and cross-spectral coherence between: (d) aspen and precipitation; (e) spruce and precipitation; (f) aspen and spruce ring widths, over the same period. Shaded bars indicate dominant spectral peaks at 0.099 and 0.160 y^{-1} (approximately 10 and 6.2 y). Spectra smoothed by Daniell smoother with spans = {3,3}. Vertical bars on spectra indicate 95% confidence interval. Dashed lines on coherency estimates indicate 95% confidence interval.

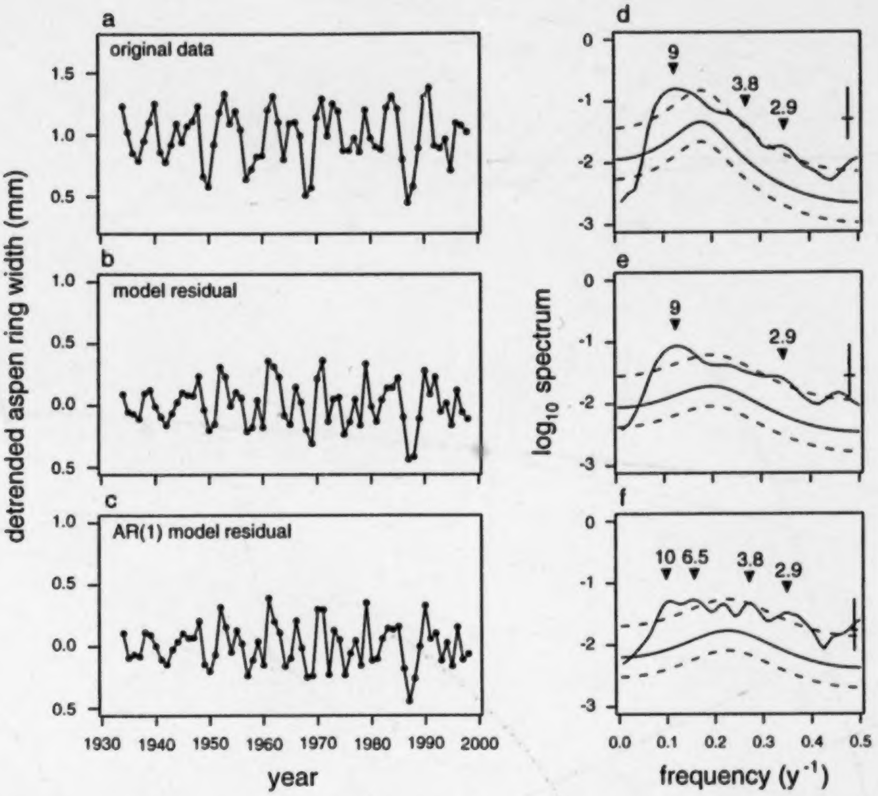

Figure 2.10. Spectral analysis of modeled grid-wide mean aspen ring width chronology. Original target data (a), residuals from linear regression on spruce, precipitation, May temperature and May snow (b), and residuals from AR(1) regression model (c). Corresponding spectra shown in (d), (e), and (f). Regression model in (b) summarized in Table 2.3. Spectra smoothed by Daniell smoother with spans={3, 5}. Horizontal and vertical lines on periodograms indicate bandwidth and 95% confidence interval assuming white null spectrum. Pink noise AR(2) spectra and 95% confidence limits on periodograms computed according to Chapman (1989). Triangles denoting statistically significant spectral peaks are labelled according to wavelength.

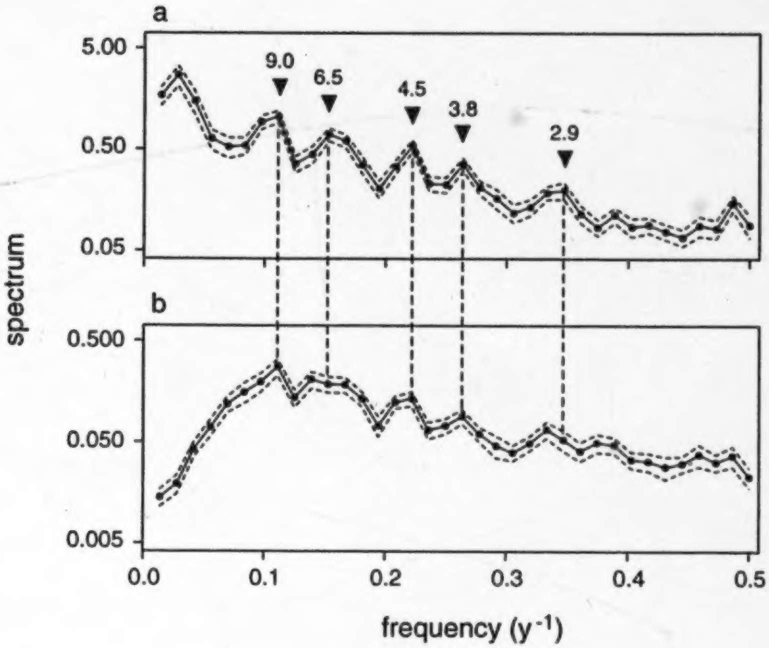

Figure 2.11. Average of unsmoothed spectra for all stand-wise aspen chronologies over the study grid 1934-1998: (a) raw aspen ring widths, (b) detrended, climate-corrected aspen ring widths. Dashed curves indicate 95% confidence intervals. Triangles denote spectral peaks near 9.0, 6.5, 4.5, 3.8, and 2.9 y. Dashed vertical lines highlight congruency of spectra.

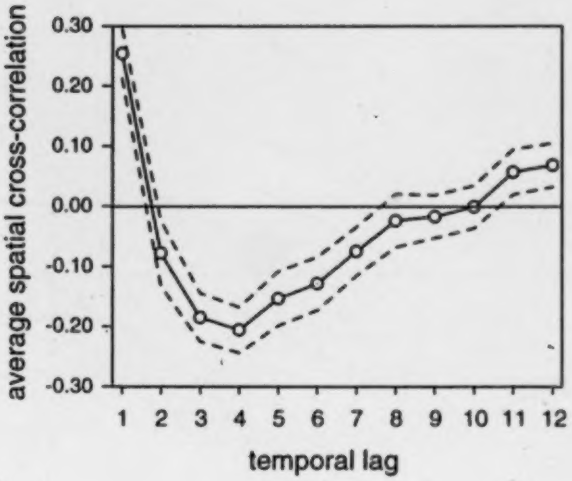

Figure 2.12. Spatiotemporal autocorrelation in detrended, climate-corrected stand-wise aspen ring width chronologies over the study grid 1934-1998. Spatial lag is fixed at zero, such that correlation coefficient measures correspondence between growth maps separated by a varying number of years.

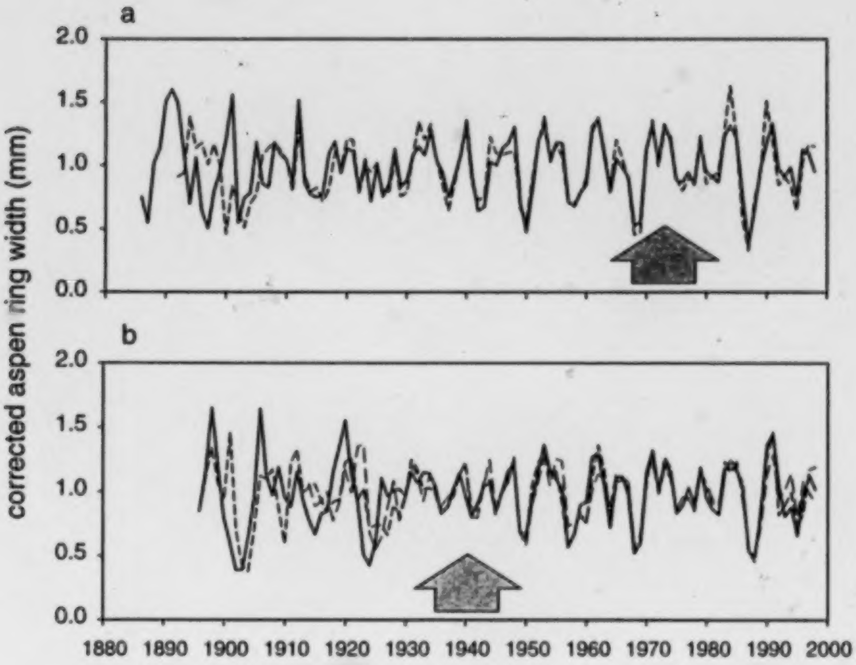

Figure 2.13. Detrended, uncorrected aspen ring width chronologies from five parts of the study grid (see Fig. 2.2). Northern section (a) includes continuous forest of Cooking Lake-Blackfoot Wildlife, Grazing and Provincial Recreation Area (solid line) and fragmented stands primarily to the southwest (dashed line). Southern section (b) includes continuous forest of Ministik Hills Bird Sanctuary (solid line) and stands in two fragmented compartments to the east and west (dashed lines). Arrows indicate approximate year of peak forest clearing in the surrounding landscape.

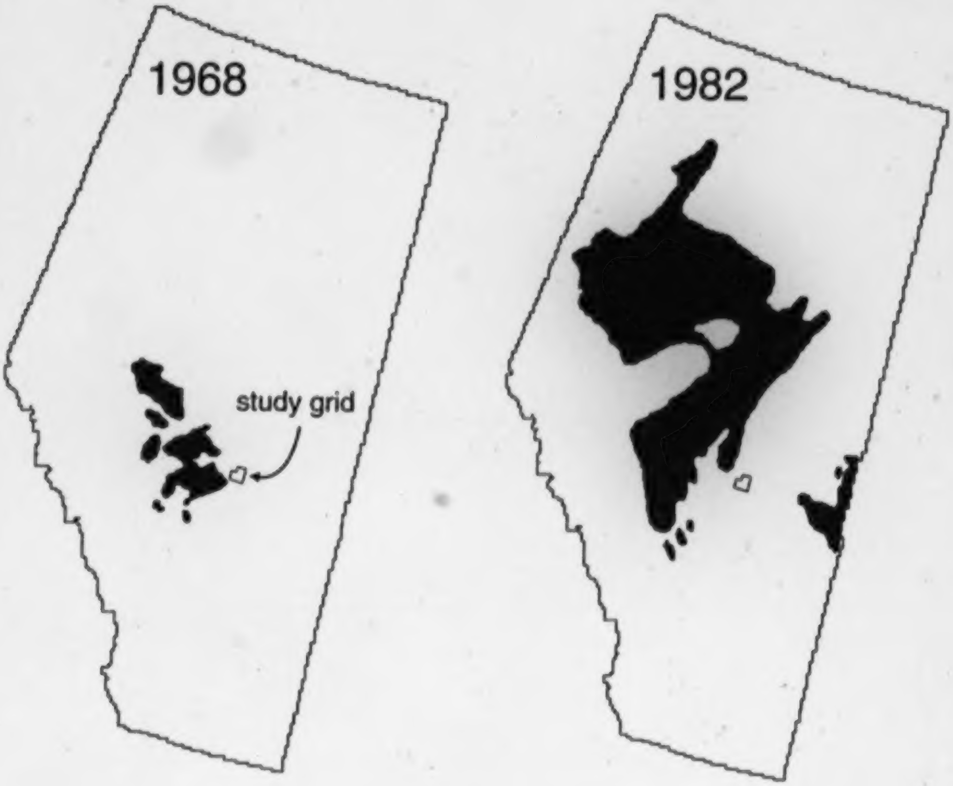
1968
study grid
1982

Figure 2.14. Severe defoliation of aspen by forest tent caterpillar in Alberta in 1968 and 1982.

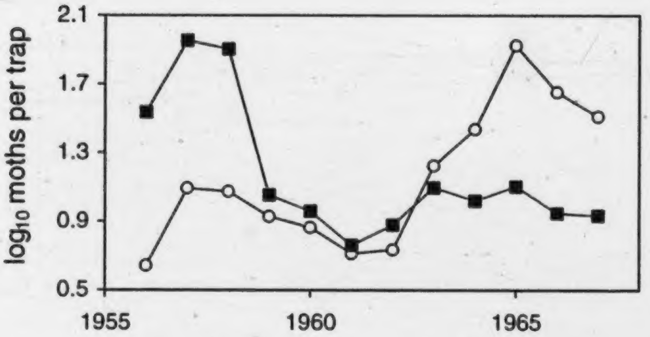

Figure 2.15. Forest tent caterpillar moths caught in light traps in northern (■) Minnesota (9 traps) and southern (○) Minnesota (10 traps). Data from Hodson's (1977) Table 3 and his Figures 22-33.

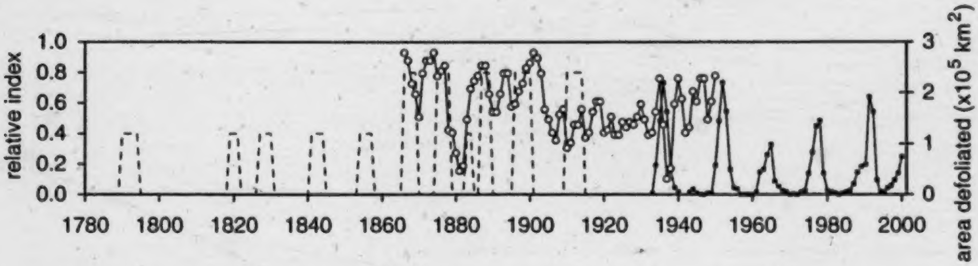

Figure 2.16. Historical records of forest tent caterpillar in Ontario. Dashed line indicates the presence of "local ravages" or "general outbreak" in eastern Canada, as described by Baird (1917). Circles indicate relative ring widths for aspen at Black Sturgeon Lake, in northwestern Ontario (Ghent 1952, Figure 1). Squares indicate total area defoliated by forest tent caterpillar: estimates for 1933-1938 based on Brown's (1938) Figures 1 and 2; rough estimates for 1939-1947 based on annual written accounts (Forest Insect and Disease Survey 1940-1948); estimates for 1948-1988 from Daniel & Myers (1995, Figure 1); estimates for 1989-1996 based on Simpson & Coy (1999); estimates for 1997-2000 based on personal communication with Gordon Howse (Forest Insect and Disease Survey, Canadian Forestry Service, Sault Ste. Marie, Ontario).

3. DENDROECOLOGICAL RECONSTRUCTION AND ANALYSIS OF FOREST TENT CATERPILLAR OUTBREAKS ACROSS NORTHCENTRAL ALBERTA

3.1 Introduction

In the prairie provinces of Canada, annual fluctuations in the growth rate of trembling aspen (*Populus tremuloides* Michx.) trees are determined largely by drought and periodic defoliation by the forest tent caterpillar, *Malacosoma disstria* (Hbn.) (Hogg 1999). In the aspen parkland region of Alberta, it is unclear which of these factors is more important because, since the 1920's, decadal outbreak cycles have been well synchronized with decadal precipitation cycles (chapter two).

This observation has led to the emergence of a scientific and a practical problem. Insect ecologists now must determine whether the correspondence between decadal drought and decadal tent caterpillar outbreaks is mere coincidence. Meanwhile, forest managers still have no good estimate of the impact of forest tent caterpillar outbreaks on aspen growth.

A positive association between forest tent caterpillar outbreaks and warm spring weather has been documented previously in western Canada (Ives 1973, 1981); however its statistical significance has been disputed (Daniel & Myers 1995). Also, its theoretical plausibility has been questioned (Roland *et. al.* 1998). While the beneficial effect of warm spring weather on tent caterpillar egg hatch and early larval survival, growth and development has been widely acknowledged (Blais *et. al.* 1955, Hanec 1966, Wetzel *et. al.* 1973, Raske 1975, Witter *et. al.* 1975, Hodson 1977, Parry *et. al.* 1998), this does not necessarily imply that population density and weather should correlate with one another, even if spring weather was the dominant source of random variation in generational survival. For, as Royama (1996, p. 46) has explained:

> "The perturbation effect ... of weather influences would show up in the population series ... only when the population is tightly regulated about an equilibrium level by a density-dependent process. It is so closely regulated

> by the density-dependent process that only the effect of density-independent weather influences show up in the population fluctuation."

Given that tent caterpillar populations are not believed to be regulated tightly about a single equilibrium level (Ives 1973, Witter *et. al.* 1975, Harmsen *et. al.* 1976, Rose 1976, Hodson 1977, Rose & Harmsen 1978, Rose & Harmsen 1981, Parry *et. al.* 1997, Myers 1998), the origin of the association between warm, dry spring weather and tent caterpillar outbreaks is a mystery.

The synchronizing influence of weather perturbations, *via* Moran's (1953) theorem, has been suggested as a possible explanation (Myers 1998); however, the point is debatable, and should be scrutinized within a more rigorous formalized framework. Of course, a spurious correlation between decadal outbreaks and drought cycles could arise through the influence of some other distantly related climatic factor, such as winter temperature. Thus the study of the nature and cause of precipitation and other low-frequency climatic processes may be of some relevance.

Either way, this confounding of factors presents a serious challenge to the quantification of outbreak impacts and to the dendroecological reconstruction of outbreaks in the parkland region of Alberta (chapter two). The problem is that a statistical approach to removing the effects of precipitation may inadvertently remove effects due to defoliation by forest tent caterpillars.

One possible solution is to study aspen growth patterns in situations where trees are less prone to drought. The boreal mixedwood region of northcentral Alberta has a wetter climate than the aspen parkland (MacIver *et. al.* 1972, Powell & MacIver 1978, Hogg 1997) and presents just such an opportunity. Here, with the influence of drought reduced, effects due to tent caterpillar defoliation may be more prominent.

In expanding the scope of study, however, several additional sources of variation might become important in outbreak reconstruction. First, given that climatic means differ over sufficiently large areas, the sensitivity of trees to fluctuations in moisture availability might vary. Second, the temporal patterns of climatic fluctuations might differ. Third, there is a greater diversity of insects other than forest tent caterpillar, such as large aspen tortrix (*Choristoneura conflictana* [Walker]) and Bruce's spanworm (*Operophtera bruceata*) that could defoliate aspen (Ives & Wong 1988). Thus the methods of dendroecological reconstruction may need to vary among municipalities.

Of course, the dynamics of forest tent caterpillar populations also may vary geographically. For example, in Ontario outbreaks frequently do not affect the far north (Sippell 1962, Daniel & Myers 1995). In Minnesota, outbreaks do not last as long in the north (*e.g.* International Falls) as elsewhere (*e.g.* Duluth) (Hodson 1977). In the prairie provinces of Canada outbreaks appear to be less synchronous and less periodic than in Ontario (Hildahl & Reeks 1960). Consequently outbreak reconstructions should be based on a large-scale sampling scheme that spans any gradients in outbreak periodicity and severity that could bias a small-scale sample.

Large-scale differences in tent caterpillar outbreak dynamics are partly a result of large-scale variation in climate and forest structure; however a substantial portion of variation in outbreak dynamics is not explained by either factor (Roland *et. al.* 1998, Cooke & Roland 2000). With so many unknown and uncontrolled factors affecting outbreak dynamics, a logical approach is to survey as widely and as intensively as possible and to include as many judiciously chosen explanatory variables as possible. This way, even if the spatiotemporal outbreak patterns do not relate to exogenous environmental gradients and fluctuations, then their endogenous structure may constitute a separate subject worthy of study. Large-scale outbreak reconstructions are also valuable because: (1) outbreak impacts in the boreal mixedwood region of Alberta have not been quantified, but are an important industrial concern; (2) large-scale outbreak patterns can be compared to small-scale outbreak patterns; (3) outbreak patterns in Alberta can be compared to patterns elsewhere.

The specific objectives of this chapter are:

(1) to determine if decadal drought is prominent in the boreal mixedwood;
(2) to determine if drought is less limiting to aspen growth in the boreal mixedwood;
(3) to quantify outbreak impacts in the boreal mixedwood;
(4) to determine if low-frequency climatic fluctuations are associated with outbreaks;

(5) to determine whether outbreak periodicity has changed over time;
(6) to compare outbreak periodicities in Alberta and Ontario;
(7) to compare outbreak patterns among various municipalities in Alberta;
(8) to determine whether forest fragmentation has reduced outbreak synchrony.

Ultimately, by exploring the relationships between large-scale outbreak patterns and exogenous environmental factors, such as climate and forest structure, it may be possible to make inferences about the nature of the endogenous processes, such as parasitism, predation, and dispersal, which govern population dynamics at local and regional scales.

3.2 Methods

3.2.1 Study sites

The study was conducted in northcentral Alberta, which straddles the southern limit of the mixed boreal forest and the northern limit of the aspen parkland. Aspen trees were sampled in 246 stands from nine municipalities arranged on a province-wide 3x3 grid that covered roughly 94 000 km^2 (Fig. 3.1). The provincial grid, in actuality, covered only the northcentral portion of the province and comprised an irregular lattice of clusters of stands. Each municipal sampling area consisted of a cluster of 7 to 24 stands that covered several hundred square kilometres. The notable exception was in the southcentral municipality, near Cooking L., where sampling was on a partial 10x14 grid of 128 stands that covered 420 km^2 of aspen parkland in Strathcona and Beaver counties (Fig. 2.2). The phrase "municipal grid" is used to distinguish this small-scale sampling scheme from the large-scale sampling scheme of the provincial grid.

3.2.1.1 Provincial grid

Three of the western-most municipalities (Dixonville, Whitecourt, Drayton Valley) were located in partially fragmented agricultural landscapes. At each of these, irregularly spaced stands were stratified into two spatially separated clusters located in predominantly continuous and predominantly fragmented forest. Stand selection on the municipal grid at Cooking L. was highly systematic and covered the full range of forest cover from continuous forest to cleared pasture. Aspen stands at Frog L. were irregularly spaced along highways in a predominantly fragmented landscape. The four remaining municipalities to the northeast (Peerless L., Fort McMurray, Athabasca, Conklin) were located in predominantly continuous forest. Here sampling was spread more evenly across townships and stand choice was limited by access routes. This hierarchy of stands, clusters, and municipalities was used as an arbitrary basis for estimating mean tree ring-width chronologies.

3.2.1.2 Municipal grid

Because the resolution of sampling was so much higher on the municipal grid, substantially more data and more types of data were acquired for small-scale analysis. Much of the municipal grid data are not described here, but are presented separately, along with detailed methods of data collection (chapter two). Some of the municipal grid data, however, are relevant to larger-scale questions, and these are included in the current chapter. The data collection methods described next provide a complete and accurate description of sampling in eight municipalities of the provincial grid, but only a partial account of sampling on the municipal grid.

3.2.2 Data collection overview

For each municipality on the provincial grid, historical weather records were used to estimate monthly precipitation (1908-1998), and historical maps of forest tent caterpillar-caused defoliation were used to estimate the percentage of area affected by moderate-to-severe defoliation (1957-1990). For each stand, aspen ring-widths were measured (boreal: 1839-1998; parkland: 1886-1998). The specifics of each data element and methods of procurement are described in turn.

3.2.2.1 Aspen rings

Aspen trees were felled in each of 246 stands. Several criteria were used in selecting plot locations and sample stems. Only stands of pure aspen, or aspen-balsam poplar, *Populus balsamifera*, were chosen. In the boreal forest, where white spruce, *Picea glauca*, is more abundant, only stands with overstorey aspen were chosen. Neighbouring stands were chosen to be at least a kilometre apart from one another. In each stand, samples were taken from the oldest, healthiest trees that could be safely felled. Trees with obvious crown damage, or numerous fungal fruiting bodies, or discoloured bark were avoided. Trees growing in close competition often had to be ignored for those more easily felled. Also, in many cases landowner preference provided additional constraints. Here sampling was sometimes limited to smaller trees with broken crowns and obvious fungal infections.

On the provincial grid, two aspen trees were felled in each stand and these were usually close enough together that they likely originated from a single clone. Sections were taken at the lowest height that was free of rot and major wound-caused distortions; this was usually between waist- and breast-height.

On the municipal grid, three aspen trees were felled in each stand. These were taken at variable distances along an elevational transect less than 100m long, regardless of clonal structure. From each stem, sections were taken up the length of the bole to the base of the crown. As cambial division is initiated at the base of the crown weeks before it is initiated at breast-height (Zimmermann & Brown 1980), it is possible to confirm annual rings missing at breast height by cross-dating with sections from crown-height. This was essential on the municipal grid because a severe forest tent caterpillar outbreak lasting from 1993 to 1995 was found, in declining stands, to result in occasional years with imperceptible growth.

All sections were dried at 40°C for several days, and sanded with a table-mounted belt-sander using 15 cm wide 50, 80, and 100 grit belts, and then polished with a palm-sized orbital sander using 150, 220, 320 and 400 grit paper. Annual growth rings were resolved using a 10-60x magnification stereo-microscope with a variety of light sources. Each ring was dated and measured to the nearest 0.01 mm using an ocular micrometer. Sectional chronologies were cross-dated by examining the cross-correlation among ring width profiles, particularly with regard to high-frequency fluctuations in ring width (Pilcher 1990). When high-frequency fluctuations did not correlate well, samples were carefully re-examined for the possible occurrence of a missing ring or a counting error (appendix one).

To estimate annual growth rates, ring widths were measured along a single radial transect across the stem section. The savings in processing time was considered worth the loss in accuracy because it was spatial variation among plots in the temporal autocorrelation structure in ring widths that was important, not the accurate estimation of mean growth rates in each year. Specifically, it was temporal variation in the 0.5 to 0.033 y^{-1} frequency range (2 to 30 y) that was of greatest interest. Any method that compromised the estimation of the autocorrelation structure in this frequency range was counter-productive. Techniques that exacerbated variation in the 0.033 to 0.0066 y^{-1} frequency range (30 to 150 y) were of no concern as these low-frequency cycles and trends would be removed regardless.

As aspen rings were being measured, they were scored as "white" or "normal". Rings that appear whitish do so because of the disproportionately high number of large vessel elements in the annual ring. There are two ways this proportion tends to vary: an increase in the number of layers of large vessels laid down in the early wood, and a reduction in the width of the late wood. Only rings of the first type were scored as white. On rare occasions, when a ring was extremely narrow, intermittent or missing, a check made on a section from the crown would reveal that a ring was present further up the bole; if this ring was white, the lower ring was scored as white. Many rings that appeared whitish with the naked eye did not appear to have the same degree of whiteness or the same cellular structure as others; these were not scored as white. Also many narrow rings appeared whitish merely because they lacked late wood growth; these were not scored as white either, although they frequently occurred the year after a white ring. This scoring policy probably underestimated the incidence of severe defoliation.

Individual ring width chronologies from each tree were detrended to remove non-stationarity due to tree-age effects and local stand effects. Two successive cubic splines with 50% frequency responses of 50 and 25 years (Cook & Kairiukstis 1990) were used to remove the low-frequency variation in growth. These relatively flexible fits were necessary because events such as canopy release and closure can cause sudden shifts in growth rates. Variation in the annual and decadal frequency range was preserved. Most of the pulse-like variation in the bi-decadal range was also retained.

Finally, the detrended tree ring width series were averaged over various spatial scales to produce mean chronologies suitable for dendroecological interpretation. Some low-frequency variation in ring widths was due to stand effects but was not removed in detrending. The asynchronous portion of this component was minimized by spatially averaging individual tree chronologies. This also served to eliminate asynchronous high-frequency noise and to enhance synchronous high-frequency fluctuations, thus strengthening the common signal in the mid- and high-frequency range.

3.2.2.2 Aerially mapped defoliation

Aerially detected defoliation by the forest tent caterpillar has been mapped in Alberta at moderately high resolution since 1957 (Forest Insect and Disease Survey 1958-1982; Ives 1971, Hiratsuka *et. al.* 1980-1982, Sterner & Davidson 1981-1983, Moody & Cerezke 1983-1986, Kondo & Moody 1987, Cerezke & Emond 1989, Emond & Cerezke 1989, 1990, Cerezke *et. al.* 1991, Cerezke & Gates 1992, Cerezke & Brandt 1993, Brandt 1994, 1995a, b, Brandt *et. al.* 1996, Ranasinghe *et. al.* 1997, 1998). National insect surveys prior to 1939 covered eastern Canada only (de Gryse 1939). From 1940 to 1956 defoliation mapping in western Canada was carried out too intermittently for time-series analysis (Forest Insect and Disease Survey 1941-1957).

Aerial surveys of aspen defoliation are supplemented by a sparse network of ground surveys to confirm defoliator identity. In several years, however, defoliation by large aspen tortrix could not be distinguished from defoliation by forest tent caterpillar because ground surveys were inadequate. This was only a minor problem for the current study because the overwhelming majority of early-season defoliation is caused by forest tent caterpillar (Ives 1981). For example, forest insect surveys within the study area show that from 1979 to 1994, defoliation by large aspen tortrix was limited to the Peace River valley in 1993 and 1994. Most of the defoliation by large aspen tortrix occurred outside the study area (*e.g.* Calgary, Millarville, Stettler, Cypress Hills, Waterton Lakes in the south and Red Earth Creek, Hinton, Wood Buffalo Park, Grande Prairie, High River to the north).

A map of the 246 dendrochronology plots was digitally overlain onto each of the provincial defoliation maps from 1957 to 1998 and the number of stands falling in the zone of severe defoliation was counted. This count was used in calculating the proportion of stands severely defoliated in each municipality. Maps were not available for 1978 and 1996 so missing values were estimated by averaging the defoliation values for the years before and after. This seemed reasonable because forest tent caterpillar populations were generally increasing in 1978 (Hiratsuka & Petty 1982) and decreasing in 1996.

3.2.2.3 Climate

3.2.2.3.1 Drought on municipal grid

For the municipal grid, a single time-series of mean daily temperature and total daily precipitation spanning 1886-1998 was assembled from daily instrumental data for two nearby weather stations: Edmonton City Centre (113.50°W, 53.55°N; 1886-1943), Edmonton Municipal Airport (113.52°W, 53.57°N; 1938-1998), (Environment Canada, Atmospheric Environment Service). Data were available for three other stations that were closer to the study area: Cooking L. Airport (113.13°W, 53.42°N; 1985-1994), Elk Island National Park (112.88°W, 53.60°N; 1967-1988), Edmonton International Airport (113.58°W, 53.30°N; 1959-1998); however, for the purposes of dendroecological reconstruction, homogeneity of temporal variation was considered more important than accuracy. In this regard, all stations showed strong coherence in temporal structure, suggesting little information would be lost in using only the two long-term stations.

Daily precipitation records were summed and temperature records were averaged over monthly time-frames in order to reduce the number of independent variables used in modeling the effect of drought on aspen growth. Initial models of aspen growth indicated that monthly mean temperatures and interactions with monthly precipitation accounted for little variation in aspen growth, suggesting precipitation alone was sufficient for modeling aspen growth.

Annual time-series of monthly precipitation had substantial high-frequency variation which resulted from 2- to 3-week periodicity in cyclonic activity. This kind of scaling effect has been termed "framing bias" because it tends to produce negative correlations between neighbouring frames (Royama 1992). As the objective was to explain low-frequency cycles in aspen growth, this high-frequency component of monthly precipitation was viewed as noise. One approach to noise reduction is to use a seasonal frame for summing monthly precipitation in order to "iron out" high frequency fluctuations in precipitation. An anomalously wet or dry seasonal precipitation index would be more indicative of variation resulting from established low-frequency (bi-decadal, decadal, and sub-decadal) atmospheric processes such as solar variability (Cook *et. al.* 1997) and large-scale oceanic effects (Cayan *et. al.* 1999), than from chance realizations of high-frequency atmospheric phenomena.

The period from March 1 to June 30 was found to be an optimal seasonal frame for relating precipitation at Edmonton to aspen growth at Cooking L. The March-June seasonal frame seemed biologically reasonable and is generally supported by the literature (Sucoff 1982, Perala 1991). Consequently precipitation was summed over that period to produce a spring precipitation index.

3.2.2.3.2 Precipitation on the provincial grid

Precipitation records elsewhere in the province spanned fewer years and were much less complete. For three municipalities (Peerless L., Conklin, Drayton Valley) the nearest weather stations with continuous, long-term daily precipitation records were more than 100km away. Those closer had short and incomplete records. For each of the remaining five municipalities, daily instrumental precipitation data were gathered from the nearest weather station with the longest, most continuous records (Fort McMurray 1949-1998, Whitecourt 1943-1989, Athabasca 1908-1998, Peace River 1908-1998 (16 years missing), Cold L. 1953-1998; Fig. 3.1). These five stations had the longest, most complete daily precipitation records in the province.

Using these daily precipitation data it appeared that the March-June seasonal frame again provided the best opportunity to explain low-frequency fluctuations in aspen growth. The March-June seasonal frame also made the best use of available records, as many weather stations in Alberta only operate in spring and early summer. Consequently this seasonal frame was used in all aspen growth models. Spatial variation in optimal seasonal framing might be expected over such large distances; however the small gains in predictive power are offset by lower parsimony. For example, it is difficult to justify the use of multiple seasonal frames among points when it is strongly suspected *a priori* that precipitation is not the only spatially variable parameter driving growth.

Estimates of monthly precipitation for the period 1908-1998 were extracted from the global historical climatological network data set that is regularly maintained by the National Climate Data Centre of the National Ocean and Atmosphere Agency (url: ftp://ftp.ncdc.noaa.gov/pub/data/ghcn/v2/v2.prcp.Z). The spatial and temporal extent of data records varied in Alberta. All available station-data were used in developing interpolated precipitation maps; however, six weather stations (Fig. 3.1) had nearly continuous and complete records: Fort Vermilion (116.0°W, 58.4°N; 1909-1985), Campsie (114.7°W, 54.1°N; 1913-1998), Sion (114.1°W, 53.9°N; 1911-1998), Lacombe (113.7°W, 52.5°N; 1908-1994), Ranfurly (111.6°W, 53.4°N; 1908-1998), and Waseca (109.4°W, 53.1°N; 1908-1998). These comprised the core of the climatic database because records for the other 90 weather stations covered much shorter time frames and exhibited numerous and large gaps in annual continuity.

Many stations exhibited annual records with missing monthly data. For example, 7.1% of all station-months had incomplete records for March through June. By estimating these missing data it would be possible to save 17.6% of the seasonally summed records that would otherwise have to be discarded due to incomplete monthly cords. Consequently it seemed worthwhile to estimate the missing monthly data.

Monthly precipitation data for March through June were kriged at high resolution (GS+, Gamma Design Software, Plainwell, Michigan) to produce replacement estimates for those station-years with partial annual records from 1908-1998. Because kriging is based purely on the spatial variogram, these replacement estimates were temporally independent and therefore did not possess the same temporal structure that would have been in the missing data. This was only a minor problem, however, as monthly precipitation is much more highly correlated among stations than among years.

Finally, because the corrected, seasonally summed instrumental precipitation estimates were accurate only in some vicinity around the weather station, these data were spatially interpolated to obtain estimates for each stand on the provincial dendrochronology grid. For each year from 1908-1998 spring precipitation data were kriged to obtain a blended estimate of seasonal precipitation at each stand. A municipal time-series was then obtained by averaging precipitation records among stands in a municipality. For eight of the nine municipalities there was a weather station nearby, so there was little difference between kriged municipal precipitation estimates and precipitation recorded at the nearest weather station. The value of kriging lay in the fact that the northcentral municipality (Peerless L.) lay more than 100 km away from each of three core weather stations to the East, West and South (Fig. 3.1).

3.2.3 Data analysis

All analyses were conducted with the R statistical package, version 1.2.1 (Ihaka & Gentleman 1996, Hornik 2001).

3.2.3.1 Outbreak reconstruction

Multiple linear regression was used to measure the explanatory power of mapped tent caterpillar defoliation on aspen growth at each provincial grid point over the period 1957-1998. Lagged defoliation was included in these models because recovery of growth rates to normal levels may require one or two years (Duncan & Hodson 1958, Churchill *et. al.* 1964) depending on the severity of the outbreak (Hildahl & Reeks 1960). All models included spring precipitation in order to provide a conservative test of the hypothesis that defoliation was driving growth. These data were also analyzed using an autoregressive model to account for possible lagged effects in endogenous factors influencing aspen growth, and to test for the presence of additional periodicity in ring widths.

For each municipality on the provincial grid, correlation analysis was used to evaluate the degree of association between spring precipitation and aspen ring widths over the period 1908-1998. The same correlations were computed for the periods 1908-1953 and 1953-1998 to determine if sensitivity to precipitation might have increased over time, as a result of climate warming. These correlations were generally low, suggesting that climate-correction by linear regression would remove very little variation from the uncorrected ring width chronologies. To clarify the reasons for poor correlations, the spectral properties of each variable were examined for each municipality.

Spectral analysis was used to test for periodicity in spring precipitation and aspen ring widths. The question was whether the poor correlations were due to substantially different temporal structures or if there was simply a lack of coherence in some key frequency range. Cross-spectral analysis was used to evaluate the degree of match between precipitation and growth fluctuations with respect to particular frequency ranges. The presence of periodic components and coherence in those frequency ranges was considered noteworthy because aspen growth might be influenced directly, through the effect of climatic fluctuations on water table levels and aspen water relations, or indirectly, through the effect of climatic fluctuations on forest tent caterpillars, which in turn defoliate aspen. Direct effects were expected at high- to mid-frequency ranges, particularly in the ENSO range (3 to 5 years); indirect effects through caterpillar defoliation were expected to be manifest primarily in the mid- to low-frequency range, particularly the decadal range (6 to 16 years).

Municipal aspen ring width chronologies were adjusted by using regression models to estimate the maximum possible effects of precipitation. Because defoliation was not used in these models, model residuals likely included some variation due to agents other than forest tent caterpillar, and excluded some variation that probably was due to forest tent caterpillar. Autoregressive moving-average (ARMA) models were used in order to simulate lagged effects due to endogenous physiological processes.

Each corrected mean municipal aspen ring width chronology was then used to correct individual stand-level chronologies within each municipality. The signal from each uncorrected mean municipal chronology was subtracted from each stand-level chronology and then the corrected signal was added back in, producing a grid of ring-width chronologies covering the period 1908-1998 which were nominally free of climatic effects. These were used in subsequent analyses.

3.2.3.2 Outbreak periodicity and synchrony

Spectral analysis was used to determine if corrected aspen ring width chronologies exhibited periodic components. Cross spectral analysis of chronologies from neighbouring pairs of municipalities was used to examine synchrony with respect to key frequencies. For consistency of comparison with climatic cross-spectral analysis, this was done over the period 1908-1998. Spectral analysis of individual chronologies was also performed on the earlier part of the boreal chronologies to test for stationarity.

To determine whether outbreak patterns differed between fragmented and continuously forested plots sampled at the three western municipalities (Dixonville, Whitecourt, Drayton Valley), aspen chronologies were compared graphically for disturbance severity and frequency. Correlation analysis was used to determine: (1) if the disturbance regime had changed over time; (2) the degree of disturbance synchrony; and (3) the degree of association between aspen ring widths and precipitation. Cross-spectral analysis of chronologies from fragmented and continuous landscapes was used to characterize any lack of synchrony.

3.3 Results

3.3.1 Outbreak reconstruction

3.3.1.1 White ring counts

Episodes of growth depression frequently coincided with the occurrence of whitish rings (Fig. 3.2). Chronologies at Dixonville, Peerless L., and Athabasca showed remarkable coincidence of white rings and growth-loss. The coincidence was less convincing at Drayton Valley, where white rings sometimes occurred with minimal growth-loss during those episodes (*e.g.* 1951 and 1964) and unconvincing at Cooking L., where sustained growth depressions at 1949-1950, 1957-1960 and 1968-1969 were rarely associated with white rings.

Of the thousands of annual rings examined, not once did a ring appear whitish because of light-coloured late wood; it was always the early wood or the entire ring that was rich in large vessel elements. This implies that whatever caused the condition occurred as soon as secondary growth was initiated in early June (Dils & Day 1950, Rose 1958), and was never caused by events in July or August. This is strong evidence that white rings were caused by tent caterpillars, which typically begin feeding in May, and not by drought, which usually occurs in the hotter and drier months of late summer.

3.3.1.2 Ring widths

Individual stand chronologies exhibited strong age-related trends and sudden shifts in aspen growth rates. Detrending of these chronologies with cubic splines removed a large portion of low frequency variation, but had minimal effect on variation in the 2 to 25-yr frequency range. When detrended plot-wise ring width chronologies were averaged for each municipality, the resulting chronologies were stationary (Fig. 3.2). The longest chronologies, which spanned the period 1837-1998, indicated 24 major large-scale disturbance episodes, each lasting more than two years. There were 8 to 16 smaller-scale disturbances of lesser duration and intensity, the precise number depending on one's definition of what constitutes a disturbance. If disturbances are not discrete events, but vary in amplitude, as suggested here, quantitative analysis of annual fluctuations by autocorrelation and spectral analysis would be highly informative.

Disturbances were somewhat synchronous across the provincial grid: large episodes, such as those in 1918, 1942, 1962 and 1982 affected several points simultaneously (Fig. 3.2). However they were also somewhat asynchronous. First, the major pulse-like episodes of growth-loss in 1918, 1942, 1962 and 1982 at Dixonville, Peerless L., Fort McMurray, Whitecourt and Conklin were in many cases followed by minor cycles of growth reduction in 1924, 1937, 1949, 1957, 1968, 1977, and 1987; yet, at neighbouring points, such as Cooking L. and Frog L., the opposite pattern as observed: the major episodes occurred at 1937, 1949, 1957, 1968 and 1987. In other words, the high-frequency cyclic component (≈5 y) was in-phase, but the low-frequency components (≈10 and 20 y) were perfectly out-of-phase. Viewed spatially, this implies major pulse-like disturbances at a given point were consistently associated with minor growth reductions at other points, and vice versa. Thus disturbance episodes tended to form a spatial gradient of impact severity, and the gradient was not spatially fixed among episodes. Second, the disturbance at Athabasca in 1939-1941 was localized, but is closely associated with the small-scale 1936-1938 episode to the south, at Cooking L., and the large-scale 1942-1943 episode to the north, at Dixonville, Peerless L. and Whitecourt. In other words, not all major disturbances were perfectly out of phase; they were sometimes lagged by a few years or less. Third, major disturbances were sometimes followed by a second major disturbance. The best example is the pair of episodes in 1982 and 1987 which affected Whitecourt, Athabasca and Drayton Valley. In contrast, Conklin, Cooking L. and Frog L. were hardly affected in 1982 while Dixonville, Peerless L. and Fort McMurray were hardly affected in 1987.

Synchrony, as measured by a correlation coefficient, is too simple a notion to characterize such a complex spatiotemporal relationship. Cross-spectral coherence between ring width chronologies is more informative because it measures the degree of correlation with respect to specific frequencies (Chatfield 1989).

3.3.1.3 Correlation and coherence with precipitation

3.3.1.3.1 Temporal analysis of precipitation fluctuations

At Cooking L., a positive correlation between aspen ring width and precipitation extended back to the 1920's, but not as far back as the earliest weather records in the 1880's (Fig. 3.3). Correlations at the other municipalities were generally much less significant over the period 1908-1998 (Fig. 3.4). Only Dixonville exhibited a correlation greater than 0.2.

For five of the municipalities (Dixonville, Peerless L., Athabasca, Conklin) correlations were at least 0.21 higher during the period 1953-1998 compared to the earlier period 1908-1953. For three of the municipalities (Fort McMurray, Whitecourt, Cooking L.) correlations differed between periods by less than 0.04. At Drayton Valley, the correlation was much lower in recent decades. Despite the low correlations, the similarity in patterns of fluctuations (Fig. 3.4) , particularly since the 1950's, suggested a single, chronology-wide correlation coefficient may be a poor measure of coherence.

Cross-spectral analysis of regional aspen ring widths and spring precipitation for 1908-1998 revealed spectral coherence peaks at 0.05, 0.11, 0.16, 0.21, 0.27, 0.37, and 0.43 y^{-1} (20, 9.1, 6.2, 4.8, 3.7, 2.7, 2.3 y) and little coherence in the remainder of the spectrum (Fig. 3.5). Notably, there was very little coherence in the 0.07 to 0.1 y^{-1} frequency range (14 to 10 y), except at Cooking L. This is in striking contrast to the precipitation spectra (Fig. 3.6), where a broad decadal peak was dominant, and lesser peaks occurred at 0.05, 0.15, 0.25, 0.37, and 0.43 y^{-1} (20, 6.7, 4.0, 2.7, 2.3 y).

There was some spatial variation in the pattern of growth-precipitation coherence. First, Cooking L. which is in the aspen parkland, was somewhat exceptional in that decadal coherence was moderate. Second, Dixonville, located in the Peace River aspen parkland northern outlier, and Peerless L., located in the boreal forest, showed extremely low coherence in the 0.07 to 0.16 y^{-1} frequency range (13 to 6.5 y), even though these were the dominant frequencies in the precipitation spectrum. (Although note a narrow spike at 9.1 y, which diminishes under greater smoothing). Therefore there were different modes of coherence in each of two areas. The northwestern mode, characterized by Dixonville and Peerless L., had peaks at 0.05, 0.22, and 0.37 y^{-1} (20, 4.5, 2.7 y) but not at

0.1 or 0.16 y^{-1} (10, 6.5 y); the southern mode, characterized by Cooking L., had peaks in all seven frequency ranges. Points in between were a blend of the two.

The patterns of growth-precipitation coherence were especially informative when compared to the detrended aspen growth spectra. Consider first the average spectrum for the nine municipal ring width chronologies (Fig. 3.7). Compared to the flat and noisy precipitation spectra, the aspen growth spectrum was dominated by low frequency variation. Such spectral "redness" suggests that aspen growth, unlike precipitation, is a low-order autoregressive process. Because of detrending, the spectrum showed little variation attributable to frequencies less than 0.05 y^{-1}. Superimposed on this asymmetrically humped pattern was an additional pattern comprising four peaks: a broad spectral peak from 0.05 to 0.1 y^{-1} (20 to 10 y) centered on 0.076 y^{-1} (13 y) and smaller local peaks at 0.16, 0.21, 0.25 y^{-1} (6.5, 4.8 and 4.0 y).

Spectra for each of the nine municipal aspen ring width chronologies followed this basic pattern; however, there was some variation in the pattern of local spectral peaks (Fig. 3.8). First, the dominant peak was broadly decadal at all municipalities (except Conklin), but the precise frequency varied from 0.06 y^{-1} (Dixonville, Frog L.) to more than 0.07 y^{-1} (Peerless L., Fort McMurray, Athabasca) to 0.1 y^{-1} (Whitecourt, Drayton Valley, Cooking L.). Hence the breadth of the decadal peak for the average periodogram for the provincial grid (Fig. 3.7). In contrast, the decadal peak in precipitation varied little among points (Fig. 3.6). Second, peaks at 0.1 y^{-1} (10 y) in Whitecourt and Drayton Valley growth spectra were sharp and strong (Fig. 3.8); yet decadal coherence with precipitation was very low (Fig. 3.5), in spite of clear decadal peaks in precipitation spectra (Fig. 3.6). Third, strong evidence for a 0.16 y^{-1} (6.5 y) peak in growth spectra was found only at Cooking L. Successively weaker peaks at that frequency occurred at Dixonville, Whitecourt, Drayton Valley, Frog L., Fort McMurray, and Peerless L. Yet precipitation spectra (Fig. 3.6) showed strong peaks at that frequency for all points (except Athabasca and Frog L.).

If spring precipitation is the main factor limiting aspen growth, then the general lack of coherence between aspen growth and precipitation spectra in the decadal and sub-decadal frequency ranges demands explanation. In contrast, the decadal pattern of fluctuations in aspen growth fits with the view that outbreaks have a variable periodicity with estimated ranges of 6 to 14 years (Sippell 1962) or 6 to 16 years (Hildahl & Reeks 1960, Witter 1979). Indeed, the estimated range of periodicity from the literature is so large that both major and minor spectral peaks at 0.0769 and 0.154 y^{-1} (13 and 6.5 y) are included (Fig. 3.7). This supports the view that forest tent caterpillar defoliation might be responsible for both low and high-frequency variations in aspen growth in Alberta.

These low and high frequencies are, in fact, harmonics: if disturbances occur every 6.5 years, then, by definition, they also occur every 13 years. Harmonic peaks are important because they imply a special temporal pattern of fluctuation. For example if two harmonic peaks are present in a periodogram, it implies that disturbances are periodic at the high frequency, and that the amplitude varies at the lower frequency, thereby producing an alternating pattern of major and minor disturbances. Recall this is, more or less, what was observed in aspen growth (Fig. 3.2).

A harmonic structure to low and medium-frequency fluctuations in aspen growth is consistent with reported temporal patterns of forest tent caterpillar outbreaks. Notably, the published range of forest tent caterpillar outbreak periodicity [6,16] is sufficiently wide that it actually includes three integral harmonic intervals: {(6,12), (7,14), (8,16)} (Fig. 3.7). Each and all of these integral harmonic intervals include the value ten, which is the most commonly cited mean periodicity of forest tent caterpillar outbreaks (Baird 1917, Hodson 1941, Sippell 1962). Two of the intervals contain the value thirteen, which has also been cited as the mean periodicity of outbreaks (Daniel & Myers 1995) and was observed to be the dominant frequency of disturbance in aspen growth in Alberta. If outbreaks do, in fact, have a harmonic temporal structure it would explain (1) the reluctance to adopt a rigid notion of outbreak periodicity (*e.g.* Hildahl & Reeks 1960) and (2) the tendency to describe the range of outbreak periodicity with intervals that span an order of magnitude (Hildahl & Reeks 1960, Sippell 1962, Witter 1979).

But if defoliation by tent caterpillars is the main factor limiting growth, then two observations need explanation. First, what caused the high degree of coherence between aspen growth and precipitation around 0.21 y^{-1} (4.8 y)? Was it drought, or mere coincidence? It could be due to tent caterpillar defoliation; however, there are no records of temporal variation in this frequency range. Furthermore, if these effects are due to tent caterpillar, then are tent caterpillar populations themselves regulated by ENSO-scale (3-5 y) variations in climate? If so, what would be the biological mechanism? Second, why is decadal coherence between precipitation and aspen growth so high at Cooking L.? Is this due to decadal drought, defoliation, or both?

3.3.1.3.2 Spatial cross-correlation between precipitation and aspen growth

Spatial correlations between patterns of growth and precipitation over the regional lattice were not consistently positive over the period 1908-98 (Fig. 3.9a). For example, there were 13 years with $r > 0.5$, and eight years with $r < -0.5$. In fact, although the mean correlation was close to zero, the distribution of correlation coefficients was bimodal (Fig. 3.9b). This suggests that precipitation is not the main factor regulating regional aspen growth.

3.3.1.4 Defoliation mapping

Disturbance episodes over the period 1957 to 1998 were closely associated with periods of severe defoliation as estimated from aerial sketch maps (Fig. 3.10). Multiple regression models of aspen ring widths in year t as a function of spring precipitation in year t and the percentage of stands lying in the zone of severe defoliation in years t and $t-1$ showed that historical defoliation was the better predictor of ring widths (Table 3.1), although much variation remained unexplained. Notably, all points except Fort McMurray had one of the defoliation terms as significant. Also, the size and significance of the precipitation coefficient was highest in the northwestern (Dixonville) and southeastern (Conklin, Cooking L., Frog L.) municipalities, which are located in the less forested parts of the aspen parkland.

Second order autoregressive models indicated that there was additional periodicity in aspen growth not explained by precipitation and defoliation (Table 3.2). The first lag was consistently positive and the second lag was consistently negative, indicating cyclic growth above and beyond the impacts of mapped outbreaks. Autoregressive coefficients were especially significant at Dixonville, Fort McMurray, Whitecourt and Athabasca.

If the effects of tent caterpillar outbreaks were accounted for in the defoliation variables, what caused this cyclic residual growth? Residuals from the AR(0) models exhibited dips in growth around the years 1957-1958, 1962-1964, 1968-1969, 1977-1978, 1980-1982, 1987-1988 (Fig. 3.11). Among pairs of municipalities, cross-spectral analysis of residuals also showed weakly bimodal spectral coherence around 0.2 and 0.1 to 0.05 y^{-1} (5 and 10-20 y) (Fig. 3.12), suggesting there was some local spatial synchrony in model residuals. The average residual also showed dips at 1957, 1962, 1968, 1977, and 1982 (Fig. 3.13a), which coincided with major disturbances (Fig. 3.2) and local outbreaks (Fig. 3.10) and led to a similar pattern of low-frequency variation (Fig. 3.13b). This suggested there was some global spatial synchrony in model residuals.

That the residuals had not only a cyclic temporal structure, but also some local and global spatial coherence suggests residual variation was due, not to sampling error, but to some other spatiotemporal process not included in the model. Important possibilities include inaccurate sketch-mapping (*e.g.* defoliation borders are hard to delineate accurately and some defoliated stands may be missed) and limited sensitivity of aerially detected defoliation (*e.g.* only severe and widespread defoliation is detectable from an airplane). The matter is crucial because results here suggest that aspen ring widths, which do not suffer from spatial infidelity, and are able to record infestations at the level of individual stems, also may be sensitive enough to record light defoliation. If so, then aspen ring widths are a better indicator of forest tent caterpillar defoliation than aerial defoliation maps. This would permit the inference that shallow dips in mean chronology growth (marked by triangles in Fig. 3.10) might be caused by sub-epidemic populations of forest tent caterpillar.

3.3.1.5 Corrected aspen chronologies

ARMA(1,1) models of aspen growth as a function of precipitation explained 9%

to 31% of the temporal variation in municipal aspen ring width chronologies over the period 1908-1998 (Fig. 3.14). The temporal structure of residual growth fluctuations differed very little from that of the original ring width chronologies (Fig. 3.15).

Due to the lack of early climatic data it was not possible to correct chronologies for precipitation effects prior to 1908; however, such effects were probably no stronger because the Albertan climate was probably no drier and no warmer during that era. Thus uncorrected aspen ring width chronologies from 1837-1908 are probably about as indicative of historical defoliation impacts as climate-corrected chronologies from later years.

Aspen growth in the boreal forest region was remarkably insensitive to temporal variation in precipitation. Even during the warmer and drier decades of the last half-century, correlations between aspen growth and precipitation were less than 0.25 for the three longest municipal chronologies (Peerless L., Whitecourt, Conklin) (Fig. 3.4). This suggests that, in the boreal region, uncorrected aspen ring width chronologies are largely indicative of the pattern of defoliation by forest tent caterpillars.

3.3.2 Outbreak patterns

3.3.2.1 Stationarity

The provincially averaged spectra of municipal aspen ring width chronologies over the entire period 1837-1998 showed peaks at 0.078, 0.106, 0.150, 0.204, 0.256, 0.294, and 0.402 y^{-1} (12.8, 9.4, 6.7, 4.9, 3.9, 3.4 and 2.5 y) (Fig. 3.16), which is similar to the provincially averaged spectra for partial chronologies from 1908-1998 (Fig. 3.7). The only difference between spectra for partial and entire ring width chronologies was that spectra for entire series (not shown) displayed a "shoulder" near 0.05 y^{-1} (20 y). Peerless L. and Conklin were the only municipalities displaying all seven spectral peaks shown in Fig. 3.7. The other seven municipalities either had one or more of these frequencies missing from their spectra (*e.g.* Whitecourt: 3.9 y; Fort McMurray: 4.9 y; Cooking L.: 12.8 y, Drayton Valley: all frequencies except 12.8 and 9.4 y) or local spectral peaks were indistinct due to overall spectral redness (Dixonville, Athabasca, Frog L.).

The statistical significance of these peaks depends on what null model is chosen. A null model based on white noise would suggest that all the low frequency peaks (12.8, 9.4, 6.7 y) were significant; a reddened null model would boost the significance of the higher frequency ranges, particularly around 2.5 y, at the expense of significance in the lower frequency range (Mitchell *et. al.* 1979). It is not clear what is the appropriate null model because little is known about endogenous processes governing aspen growth and possible lagged effects. If, in the absence of disturbance, growth is temporally autocorrelated, a reddened null spectrum would be appropriate.

The statistical significance of cyclic components is not a crucial issue, however, because the goal of the analysis is not to test whether disturbances are cyclic, but to compare temporal patterns in space. That there is any temporal structure consistent among municipalities is in itself a "significant" result. Unless it can be shown that different processes account for different peaks, the specific frequencies are not especially meaningful. For example, that there is a spectral peak at 12.8 y is noteworthy because this is the dominant frequency of tent caterpillar outbreaks in Ontario (Daniel & Myers 1995). This is not intended to suggest that populations in Alberta and Ontario are cyclic with a 12.8 year periodicity; this would be a drastic oversimplification. On the other hand there may well be minor spectral peaks in Ontario outbreaks that have simply not yet been described. The key point, however, is that there is a correspondence in some frequency range which does not correspond to known climatic variability.

Subtle differences between spectra for full and partial chronologies were due to non-stationary aspects of three boreal chronologies that extended back to 1839. These showed a transition in outbreak dynamics occurring around 1900 (Fig. 3.2). Spectral analysis revealed that prior to 1900, the dominant spectral peak was between 0.15 and 0.18 y^{-1} (6.7 and 5.6y) and after 1900 the dominant frequency shifted to the 0.05 to 0.1 y^{-1} (20 to 10 y) frequency range (Fig. 3.17). A plot of the average of the three chronologies suggests that the change was not sudden, but gradual, occurring over the period 1870 to 1910 (Fig. 3.18a, b). Spectra differed in the 0.12 to 0.17 y^{-1} (8.3 to 5.9 y) frequency range, but peaks around 0.1 and 0.2 y^{-1} (10 and 5 y) were present both before and after 1900 (Fig. 3.18c, d).

3.3.2.2 Synchrony

3.3.2.2.1 Cross-spectral coherence among neighbouring municipalities

Cross-spectral analysis of climate-corrected aspen ring width chronologies from neighbouring pairs of municipalities indicated consistently high coherence in the 0.04 to 0.08 y^{-1} (25 to 12.5 y) frequency range, consistently low coherence right at 0.1 y^{-1} (10 y), and a variable pattern of high coherence at one or more higher frequencies, especially: 0.15, 0.22, and 0.28 y^{-1} (6.5, 4.5, and 3.6 y) (Fig. 3.19). Thus major, bi-decadal outbreaks were well-synchronized among neighbouring municipalities but higher frequency eruptions were not. For example, had outbreaks been perfectly synchronized among municipalities, all cross-spectra would have shown high coherency across the decadal band from 0.0625 to 0.167 y^{-1} (16 to 6 y).

This pattern of coherence suggests that the distinction between "outbreak dynamics" and "population dynamics" may be a useful one because different kinds of factors operating at different spatial scales may be responsible for synchronous, large-scale, bi-decadal outbreaks and asynchronous, localized, sub-decadal infestations. The degree of asynchrony is sufficiently high that there are limits to what can be learned from a temporal analysis with spatially aggregated chronologies. Chapter six investigates more thoroughly the spatiotemporal structure of outbreaks and attempts to model them.

3.3.2.2.2 Distance-dependent synchrony decay

If the temporal pattern of outbreaks changed over time, was there also a change in distance-dependent synchrony? This might be expected if, for example, increased large-scale forest fragmentation was serving to uncouple local populations from one another, thereby desynchronizing forest tent caterpillar populations in adjacent municipalities. Outbreak synchrony did decay as a function of distance between municipalities; however, over the 46-year period from 1953-1998 synchrony was actually higher than in the 46 years previous, from 1908-1953 (Fig. 3.20a, b).

Increased synchrony in aspen growth fluctuations over time was not a result of increased climatic synchrony because precipitation synchrony showed the opposite trend. Although spring precipitation was highly spatially autocorrelated and showed a similar pattern of distance-dependent synchrony decay, synchrony was slightly lower through 1953-1998 compared to 1908-1953 (Fig. 3.20c, d). It was not determined to what extent this was a result of the greater availability of instrumental precipitation data in the later period and the greater reliance on kriged data in the earlier period.

The pattern of increased outbreak synchrony and stronger distance-dependent decay was largely due to the severity of province-wide outbreaks in 1957-1963 and 1982-1988 (Fig. 3.2). Note it is not merely that apparent impacts earlier in the chronology underestimate the true severity of outbreaks: survivorship bias resulting from differential mortality of defoliated aspen appears to be negligible (chapter four). With the comparison between years so heavily dependent on only two events, the data should not be over-interpreted. Cross-correlations are poor indicators of synchrony when cyclic time-series data are short relative to the principal wavelength and when the oscillatory signal is subject to severe noise or stochastic perturbation (*e.g.* Ranta *et. al.* 1997, Cooke 1998).

3.3.2.2.3 Disturbance synchrony among forest types within municipalities

The frequency and duration of disturbances over the period 1911-1998 did not differ among fragmented and continuously forested landscape-clusters within municipalities (Fig. 3.21). Although aspen growth was correlated between landscape types (r=0.64, 0.50, 0.54, 0.67 for Dixonville, Whitecourt, Drayton Valley, Cooking L.), disturbance pulses were not perfectly synchronous. Instances of asynchronous disturbances include: Dixonville 1942-1947, 1967-1978; Whitecourt 1928-1934, 1958-1964; Drayton Valley 1941-1946, 1949-1953, 1985-1987; Cooking L. 1922-1925 (Fig. 3.21).

Correlations between aspen growth rates and spring precipitation were higher at fragmented clusters than at continuously forested clusters $r = 0.46, 0.17, 0.22, 0.45$ *versus* $r = 0.23, 0.06, -0.05, 0.44$ for Dixonville, Whitecourt, Drayton Valley, Cooking L. respectively). Notably, disturbances at 1925, 1929, 1945, and 1950 were stronger in fragmented clusters, and coincided with low precipitation. Meanwhile disturbances in the continuously forested clusters often were not coincident with either low precipitation or growth dips in the fragmented clusters (*e.g.* Dixonville 1914-1916, 1941-1943, 1980; Whitecourt 1915-1916, 1933-1935, 1941-1942, 1946, 1951-1954, 1961-1963; Drayton Valley 1925-1927, 1944-1946, 1952,-1953). Correlations between chronologies and correlations with precipitation did not differ between the 46-year periods 1908-53 and 1953-98 (results not shown).

That correlations between aspen growth and precipitation were higher in fragmented forests is consistent with the observation that the fragmented plots were located 10-50 km from the border of the aspen parkland forest region (Fig. 3.1), which is a climatic region of moisture deficit (Hogg 1997). This interpretation is corroborated by the observation that precipitation responses at Cooking L. did not differ between forest types even though distance between continuous and fragmented plots was comparable (20-40 km). This illustrates a limitation in the methods used for correcting for drought effects on aspen. Mean chronologies should be estimated for plots with similar microclimates, even though it is conceptually simpler and more convenient to develop chronologies for naturally aggregated clusters of plots, such as at the municipal scale. It is unlikely, however, that the temporal pattern of aspen growth fluctuations would be much different were the effects of drought removed because much of the asynchrony is likely due to the spread of outbreaks across stands within each municipality, a topic pursued further in chapter six.

3.4 Discussion

3.4.1 Chronology interpretation

Although there are many factors that affect aspen growth, it is doubtful that, at the large spatial and temporal scales of this study, they collectively explain as much variation as do forest tent caterpillar outbreaks. The temporal coincidence of white rings and growth dips in aspen chronologies from 1895-1998, the spatial correspondence between regionally mapped aspen growth and defoliation from 1957-1998, and the lack of coherence between aspen growth and decadal variation in precipitation from 1908-1998, collectively suggest that aspen growth across northcentral Alberta is limited primarily by defoliation by insects. The primary aspen defoliator is undoubtedly the forest tent caterpillar because no other species attains such spatially extensive and temporally prolonged outbreaks (Ives 1981).

While it is unlikely that every single dip in aspen growth in every municipality is the result of a forest tent caterpillar infestation, it is likely that the overall pattern of aspen ring width fluctuations is probably representative of the history of tent caterpillar outbreaks. The evidence for this interpretation is not unequivocal, however, and some of the more contentious issues are discussed in turn.

3.4.1.1 White ring anomalies

White rings did not always coincide with severe and prolonged episodes of growth reduction. For example, at Drayton Valley, white rings were frequent in 1951 and 1963, but the municipality-wide aspen growth rate was not extremely low. And conversely, at Cooking L., even after accounting for precipitation effects, aspen growth rates were abnormally low in 1937, 1950, and 1968 but white rings were rare.

White rings were common at Cooking L. during the outbreak years 1992-1995, proving that aspen there are capable of forming white rings. Perhaps white rings are less common at Cooking L. simply because caterpillar populations there do not attain as high a density. This seems unlikely given the high densities attained in 1994 and 1995. But perhaps the present is not indicative of the past: perhaps outbreaks now are worse than they used to be at Cooking L. This hypothesis, however, leads to a different quandary: if population densities in the past were lower, then why were impacts so severe? Perhaps the apparent severity of defoliation impacts at Cooking L. is exaggerated by the exceptional degree of synchrony of disturbance among stands sampled there (Fig. 3.21d). For example mild, large-scale disturbances that are highly synchronized may have a stronger region-wide impact on growth than severe, localized disturbances; fluctuations that are asynchronous among stands, when averaged across a municipality, tend to cancel each other out. Indeed, high variability of stand-level impacts resulting from poorly synchronized outbreaks may explain why, at Drayton Valley, aspen ring widths fluctuated less wildly than at other municipalities and corresponded poorly to local white ring counts (Fig. 3.2).

White rings were more common in later portions of chronologies, such as 1982 and 1987 (Fig. 3.2), yet it is doubtful that outbreaks suddenly intensified. A decreasing frequency of white rings could be a result of survivorship bias induced by differential mortality of defoliated trees. Survivorship bias seems too weak to effect such drastic non-stationarity in aspen ring width patterns (chapter four); however white ring occurrence may be more sensitive to survivorship bias. For example, those trees with white rings may be substantially more at risk of dying compared to trees that experienced growth reduction but did not produce a white ring.

3.4.1.2 Weak predictive power of aerially mapped defoliation

Aerially mapped defoliation was significantly related to aspen growth but it explained little variation (Table 3.1). The poor fit of defoliation models to tree growth data (Fig. 3.10) might be a result of dispatching, searching, detection, and mapping biases. For example, defoliation impacts may be underestimated at the stand- and tree-level if : (1) surveyors are not be dispatched until a year after the very first signs of defoliation; (2) surveys are less intensive in remote locations (*e.g.* Fort McMurray); (3) infestation detectability is lower in mixed coniferous forest (*e.g.* Peerless L.); (4) outbreak extent is mapped at a higher resolution in agricultural landscapes (*e.g.* Cooking L.). These biases would be especially important in sub-epidemic or patchy populations, which would affect growth locally but might escape aerial detection.

3.4.1.3 Drought effects

There is little evidence that drought is a major factor regulating aspen growth fluctuations across northcentral Alberta. First, if drought were a localized process, one would expect annual regional maps of spring precipitation to correlate with annual regional maps of aspen growth, but this was not the case. In fact, these variables were sometimes negatively correlated. Second, a prominent decadal cycle in spring precipitation was found in Alberta, yet coherence between precipitation and aspen growth was remarkably low around 0.1 y^{-1} (10 y). This is especially significant given aspen growth was dominated by periodicities in the range 16 to 6 y. If drought were limiting aspen growth, one would expect much higher decadal coherence between aspen growth and precipitation.

One could argue that March-June precipitation is not a biologically accurate indicator of drought. Yet this index did explain some variation in aspen growth at Cooking L. It may well be that boreal aspen do not respond to precipitation in the same manner as parkland aspen, and that a different seasonal frame or a non-linear model or a process-based model of physiological preconditioning would better represent boreal aspen responses to precipitation. This view presents an epistemological dilemma: one can only be confident that a drought index is good when it is found to be a good predictor of growth; but if one had to search among millions of predictors, then the collective chance of falsely concluding the predictor is causative is very high.

In correcting chronologies for climatic effects, any static algorithm is bound to be inappropriate because a changing climate implies limiting factors may also change. For example, aspen at Cooking L. seem to have become increasingly moisture-limited with time (Fig. 3.10), perhaps as a result of increasing summer temperatures (Fig. 2.3). Moreover, because the onset of moisture limitation may have varied across the province, a temporally dynamic correction algorithm ought to be spatially explicit.

3.4.2 Outbreak patterns

3.4.2.1 Outbreak cycles

Outbreaks were roughly cyclic with a period of 10 to 20 years. The primary low-frequency oscillation had a periodicity close to 20 in the boreal forest to the north (Dixonville, Peerless L., Fort McMurray, Athabasca), and close to 10 in the boreal-parkland transition (Whitecourt, Drayton Valley, Conklin, Frog L.). At all these grid points, spectral peaks in this low frequency range were sufficiently broad that they spanned almost an order of magnitude. Hence the roughness of cyclicity and the irregularity in amplitude, with large outbreaks typically being followed by smaller outbreaks. Temporal patterns at Peerless L. and Athabasca show this particularly well: bi-decadal outbreak pulses around 1941, 1962, and 1982 bracket smaller episodes at 1946, 1949, 1952, 1958, 1968, 1972, 1978. Such irregularity suggests outbreaks are not merely large-scale population cycles being driven by lagged effects of parasitism.

A 20-year outbreak cycle seems to be outside the described range of outbreak periodicity in North America. However, this may be partly a scaling issue. To illustrate, even though the mean province-wide outbreak periodicity is 13 years in Ontario, the periodicity in any one district can be somewhat less frequent due to the occasional absence of local outbreak (Daniel & Myers 1995). For example, outbreak periodicity in Thunder Bay district is substantially higher than elsewhere because the large-scale outbreak that lasted from 1965 to 1968 did not affect that area (Cooke & Roland 2000).

There appears to be a gradient in outbreak periodicity from 20 years in the northern boreal forest to 10 years in the southern aspen parkland. Forest tent caterpillar outbreaks in the far north of Ontario also seem to rather infrequent (Daniel & Myers 1995), supporting the view that outbreak periodicity may vary as a simple function of latitude. The cause of this gradient is unknown, but it could be due to a gradient in winter climate because winter temperature is an important factor affecting egg survival (chapter eight). Of course, other spatially structured variables, both endogenous and exogenous, may be responsible for the gradient in outbreak periodicity (*e.g.* Roland *et. al.* 1998).

A remarkably similar latitudinal gradient in tree ring width periodicity has been reported for *Pinus longaeva* growing on dry sites in Russia (Kocharov 1990). The transition from 20-year cycles in pine growth in the north to 10-year cycles in the south has been linked to low-frequency solar variability, which is thought to influence precipitation patterns through latitudinal shifts in meridional versus zonal patterns of upper atmospheric flow. Drought is one means by which solar variability could influence growth rates of terrestrial plants (Cook *et. al.* 1997). However, solar variability, through its impact on upper atmospheric flow, could also affect surface-level air temperatures (Schuurmans 1979), which in turn mediate rates of insect development, feeding, and survival. Forest tent caterpillar population dynamics may be largely driven by the effect of low-frequency variation in winter temperature on egg survival (chapter nine).

3.4.2.2 Outbreak synchrony

The cyclic spatiotemporal pattern of outbreaks on the municipal grid was sufficiently synchronous (chapter two) that it is fairly compatible with theoretical predictions of Ricker-Moran cellular automata, which tend to perfect synchrony for sufficiently high dispersal rates and sufficiently strong lagged predator-prey interaction and sufficiently mild random perturbations (Kaneko 1998). There was some asynchrony that resulted from the rapid spread of outbreaks across the grid; however, the resolution of sampling was sufficiently high that asynchrony at this scale might be a sign of microscopic pattern formation, which is not incompatible with Ricker-Moran dynamics (Solé & Bascompte 1998).

On the other hand, at least some of that local asynchrony was associated with regional asynchrony. For example, the East-West spread of the 1987-1988 outbreak across the local grid was part of the regional westbound wave of outbreak that emerged at Frog L. in 1986, passed through the Cooking L. area in 1987-1988, collapsing at Frog L. in 1988, and moved on to Drayton Valley in 1989 while collapsing at Cooking L. The 1922-1926 outbreak on the municipal grid showed a similar pattern of spread. This suggests that asynchrony at the local scale was not merely due to microscopic spatial pattern formation resulting from host-parasitoid diffusive instability.

Outbreaks at the provincial scale were substantially less well synchronized.

Severe outbreaks occurring at intervals of 12 to 20 years were fairly well synchronized, although the bi-decadal 1940 outbreak at Athabasca was not perfectly synchronized with the bi-decadal 1942 outbreak to the north and south, and the bi-decadal 1924 outbreak at Athabasca, Cooking L. and Drayton Valley was not well synchronized with the bi-decadal 1918 outbreak to the north. As observed on the municipal grid, smaller episodes of growth-loss occurring at intervals of 6 to 10 years and 3 to 5 years were poorly synchronized. Such asynchrony is unlikely to be the result of host-parasitoid diffusive instability because of the large distance involved (10^5 to 10^6 m) relative to the likely scales of host and parasitoid movement (10^2 to 10^3 m).

If sub-populations in each municipality are regulated by the same non-chaotic, density-dependent processes, and if municipalities are close enough together that: (1) they are subjected to highly correlated temporal patterns of climatic fluctuations, and (2) the rates of host and parasitoid migration between sub-populations are not negligible, then, in theory, these populations should fluctuate in perfect synchrony. That they do not suggests at least one of these assumptions is incorrect.

3.4.3 Population dynamics

3.4.3.1 Variability in cycle amplitude

The most curious feature of the aspen ring width chronologies is the pattern of large outbreak pulses being followed by one, two, or three smaller episodes of growth-loss at intervals of 3 to 5 years. Temporal patterns at Peerless L. and Athabasca show this particularly well: bi-decadal outbreak pulses around 1941, 1962, and 1982 bracket smaller disturbance episodes at 1946, 1949, 1952, 1958, 1968, 1972, 1978. These smaller episodes are sometimes in phase with disturbances elsewhere on the provincial grid.

These weakly synchronized 5-year cycles in growth-loss are probably not caused by drought, but are probably due to defoliation by forest tent caterpillars. If the smaller boreal episodes were perfectly in phase with large pulses in the parkland, they might simply be due to regional drought effects that were not detected in our analyses; however, the phasing is not close enough. For example, the 1952 regional episode comprises local incidents in 1951 at Athabasca and in 1953 at Peerless L.; the 1968 regional episode comprises local incidents at Peerless L. in 1966 and 1969. The weakly synchronized, smaller episodes of growth-loss are also probably not due to asynchronous local drought either. If this were the case, the static spatial variation in drought vulnerability would lead to a static pattern of growth loss: plots that escape disturbance should always escape disturbance. However, this was not observed; the disturbance affected some plots at some times and other plots at other times. Thus it appears that the disturbing process must be spatially heterogenous and contagious at both large and small scales. That white rings are associated with some of these minor growth depressions, such as at Conklin 1948, Drayton Valley 1951, Fort McMurray 1954, Athabasca 1956, Drayton Valley 1964, Dixonville 1968, Conklin 1973, Peerless L. 1977, suggests that these high-frequency, low-impact disturbances are due to insect defoliation. The regularity of these disturbances and the association with forest tent caterpillar outbreaks at neighbouring grid points suggests these minor disturbance episodes are due to sub-epidemic populations of forest tent caterpillar.

3.4.3.2 Spatiotemporal eruptivity

That outbreaks sometimes occur rather suddenly and exhibit non-epicentric patterns of spread at both local and regional scales supports an eruptive hypothesis of forest tent caterpillar outbreak occurrence. On the other hand, population cycles seem too variable in amplitude and too highly periodic to be governed solely by a simple eruptive mechanism. But if eruptivity is mediated by a slow-changing variable such as forest dynamics or non-lethal disease transmission, this might explain why some population cycles result in epidemic outbreaks while others result in sub-epidemics. And if population collapse is assisted by density-dependent perturbation effects, this would enhance the regularity of oscillations. The hypothesis is expressed most clearly in the mechanistic simulation models proposed by Rose (1976).

A similar eruptive model has been proposed to explain spruce budworm outbreaks (Ludwig *et. al.* 1978). Royama (1996) rejected this theory, arguing that:

(1) budworm early larval survival is not as sensitive to weather as the model supposed, and the concept of cycles in spring climate is unfounded;

(2) food shortage is not a universal cause of budworm population decline;

(3) budworm moth invasions do not prevent population decline;

(4) the concept of epicentric outbreak spread is founded on the illusion of population density gradients suggested by large-scale maps of categorical defoliation intensity;

(5) budworm late larval survival does not exhibit as sigmoid a pattern of density-dependence as the model supposed; hence there is no empirical basis for presuming a multiple-equilibrium structure.

These criticisms are less applicable in the case of the forest tent caterpillar. First, overwintering survival of forest tent caterpillar eggs depends on temperature and larval food quality, and larval food quality decreases when high density populations are forced to forage in the understorey. Thus cold winter weather, cyclic or not, is a common proximal cause of population collapse (chapter eight). Second, dendroecological outbreak reconstruction shows that patterns of forest tent caterpillar outbreak spread are not merely epicentric but have a joint spatiotemporal pattern of flow. Third, whether endemic populations can be perturbed to an epidemic state by small amounts of immigration at first seems unlikely because of concomitant high predation (Parry *et. al.* 1997); however, the density-dependent responses of natural enemies at low host densities has not been thoroughly investigated. Indeed, a single equilibrium process may generate oscillations that appear eruptive if the reproduction surface is sufficiently non-linear. In summary, then, there is no basis for rejecting an eruptive hypothesis of forest tent caterpillar outbreak occurrence.

It may be that modulation of a non-linear predator-prey interaction is a sufficient explanation for observed variability in outbreak amplitude. And, if moth dispersal does not occur over large distances, then (a) slight departures from perfect local synchrony (*i.e.* non-epicentric local outbreak spread) might be due to a weak effect of immigration on boosting growing populations and sustaining declining populations, and (b) large departures from regional synchrony might be due to the lack of dynamic homogenization *via* dispersal coupled with the weakness of phase-locking *via* the Moran effect. Under this scenario, there would be no need to suppose that outbreaks spread by an eruptive, multiple-equilibrium mechanism.

Even if the eruptive outbreak hypothesis is mechanistically inappropriate in the case of the forest tent caterpillar, it seems empirically useful to distinguish between population cycles and outbreak cycles. The distinction may not be relevant for understanding how outbreaks occur, but it could be relevant for describing how populations are synchronized at local and regional scales. For example, the biological factors that cause local population synchrony may be different from those that cause regional outbreak synchrony, and the mechanisms behind each (phase-locking, dynamic homogenization, period-forcing) might be different as well.

3.4.3.3 Effects of forest fragmentation and climate change

Distance-dependent synchrony decay has not increased on the provincial grid, despite substantial forest fragmentation throughout the aspen parkland. Thus it does not appear that populations are being decoupled by forest fragmentation. On the other hand, boreal outbreak dynamics began changing some time between 1870 and 1920, when settlement was beginning on the northern Canadian prairies. This was also around the time that winter climate began warming, so it is unclear to what extent the shift in outbreak dynamics might be caused by anthropogenic or climatic factors.

3.5 Conclusion

Aspen growth across northcentral Alberta seems to be predominantly limited by defoliation caused by the forest tent caterpillar. Outbreaks in Alberta are highly variable in time and space and constitute a meso-scale disturbance (*sensu* Swetnam & Betancourt 1998) in that they appear to be synchronous over tens of kilometres but poorly synchronized over hundreds of kilometres. Outbreaks in the boreal mixedwood region are sufficiently severe and well-synchronized that they can cause large-scale reductions in aspen growth rates to nearly negligible levels for periods of two years. Outbreaks in the parkland region appear less well synchronized and losses are therefore more difficult to estimate and are not easily compared between regions. Volume losses in canopy trees may be compensated to some degree by gains following disturbance, particularly in the understorey. Such effects should be quantified because they may influence the predictions of wood supply models upon which harvest schedules are based.

Outbreak patterns in Alberta seem less synchronous than those reported for Ontario. However, this study highlights some limitations in the use of aerial defoliation mapping data that likely apply to the Ontario data as well. Initial dendrochronological examinations suggest that populations in Ontario are not as synchronous as outbreak maps for that province suggest; there appear to be minor episodes that occur between the major detectable ones (chapter two).

It is suggested that minor episodes of depressed aspen growth are not due to drought but to sub-epidemic populations that escape detection by aerial defoliation mapping. If the minor episodes of growth-loss that precede and follow major outbreaks are indeed due to sub-epidemic caterpillar populations, it implies that something is missing in our basic understanding about the deterministic processes governing population fluctuations. It is important to resolve the matter because it is the severity, regularity and synchrony of these phenomena which have fostered classical views such as limit cycles driven by a predator-prey interaction (Nicholson & Bailey 1935), cusp-catastrophes driven by a periodic trigger (Murray 1993) and stochastic predator-prey oscillations about a dynamic equilibrium point (Royama 1992).

If the principal oscillation of forest tent caterpillar populations is due to lagged interactions with parasitoids, then the nature of the interaction must be substantially more complicated than most models assume. The weakly asynchronous outbreak patterns at the local scale and the highly asynchronous patterns at the regional scale suggest that outbreaks are not merely the result of limit cycles driven by a simple predator-prey interaction. This sort of weak synchrony is not predicted from theoretical models of population dynamics that take into account Moran's effect of synchronization of intrinsically identical oscillators *via* spatially autocorrelated independent random perturbations and Barbour's effect of synchronization of a metapopulation *via* dispersal among sub-populations. Therefore, even at small spatial scales, it is questionable to what extent host and parasitoid populations are:

(1) inter-connected by migration among forest patches;
(2) jointly influenced by spatially autocorrelated perturbations;
(3) intimately coupled in a specialist predator-prey interaction.

A careful examination of the spatiotemporal nature of long-term outbreak dynamics across large and small spatial scales should help to evaluate the applicability of spatially explicit ecological theory to the problem at hand. Determining the scales at which emergent properties may be resolved would constitute a significant step toward an ultimate explanation for the occurrence of forest tent caterpillar outbreaks.

The nature of forest tent caterpillar outbreaks has changed only a little despite large-scale climate warming and severe forest fragmentation. However, changes in dynamics are expected to occur once ecological and climatic tolerance-thresholds are exceeded. If forest tent caterpillars or their natural enemies are able to adapt quickly to environmental changes, then evolutionary adaptation may lead to unanticipated dynamic consequences. The possibility is accentuated by evolutionary feedback: ecological circumstances provide the basis for natural selection; natural history traits provide the parameters that govern population dynamics; density-dependent interactions provide the arena for intra- and inter-specific competition. Expectations for increased predictive power should be tempered by the knowledge that future outbreaks may not follow the course of the past and that even process-based models have structural limitations that prevent them from being universally applicable.

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Table 3.1. Standardized regression coefficients and coefficient of determination for regional defoliation models. Standard error of coefficient estimates shown below in parentheses.

municipality	defoliation	lagged defoliation	precipitation	r^2
Dixonville	-0.122 (0.173)	-0.519^{***} (0.173)	0.406^{***} (0.116)	0.49
Peerless L.	-0.444^{***} (0.141)	-0.178 (0.139)	0.130 (0.139)	0.23
Fort McMurray	0.000 (0.164)	0.0600 (0.160)	0.162 (0.164)	0.00
Whitecourt	-0.398^{**} (0.166)	-0.255 (0.166)	0.220^{*} (0.127)	0.34
Athabasca	-0.461^{*} (0.176)	-0.110 (0.176)	0.205 (0.132)	0.29
Conklin	0.328^{**} (0.146)	-0.826^{****} (0.157)	0.317^{*} (0.115)	0.48
Drayton Valley	-0.365^{**} (0.171)	-0.396^{**} (0.175)	0.111 (0.121)	0.45
Cooking L.	-0.221 (0.141)	0.255^{*} (0.146)	0.552^{****} (0.133)	0.36
Frog L.	0.331^{*} (0.172)	-0.614^{****} (0.172)	0.420^{***} (0.130)	0.31

**** $p < 0.001$, *** $p < 0.01$, ** $p < 0.05$, * $p < 0.1$

Table 3.2. Regression coefficients and Akaike Information Criterion (AIC) for regional second-order autoregressive (AR(2)) defoliation models. Standard error of coefficient estimates shown below in parentheses. AIC for the non-autoregressive multivariate model (*i.e.* AR(0)) shown for comparison.

municipality	defol.	lagged defol.	precip.	α_1	α_2	AIC AR(2)	AIC AR(0)
Dixonville	-0.0017 (0.0010)	-0.0025 (0.0010)	0.0018 (0.0005)	0.54 (0.15)	-0.37 (0.15)	-23.1	-15.9
Peerless L.	-0.0083 (0.0024)	-0.0030 (0.0024)	0.0004 (0.0004)	0.25 (0.16)	-0.27 (0.15)	-18.2	-17.3
Fort McMurray	-0.0023 (0.0064)	0.0005 (0.0062)	0.0000 (0.0006)	0.81 (0.15)	-0.34 (0.15)	-33.9	-15.7
Whitecourt	-0.0033 (0.0011)	-0.0011 (0.0011)	0.0012 (0.0004)	0.61 (0.14)	-0.42 (0.14)	-26.0	-13.6
Athabasca	-0.0030 (0.0012)	-0.0005 (0.0011)	0.0008 (0.0004)	0.60 (0.14)	-0.52 (0.13)	-11.6	3.5
Conklin	0.0016 (0.0010)	-0.0045 (0.0010)	0.0014 (0.0002)	0.39 (0.14)	-0.47 (0.14)	-62.2	-56.3
Drayton Valley	-0.0030 (0.0010)	-0.0045 (0.0010)	0.0003 (0.0060)	0.66 (0.16)	0.09 (0.17)	-29.1	-14.4
Cooking L.	-0.0005 (0.0007)	-0.0016 (0.0007)	0.0019 (0.0003)	0.48 (0.14)	-0.48 (0.14)	-25.5	-17.5
Frog L.	0.0016 (0.0011)	-0.0035 (0.0011)	0.0020 (0.0004)	0.22 (0.18)	-0.22 (0.17)	-18.4	-18.9

α_1: first-order autoregressive parameter; α_2: second-order autoregressive parameter

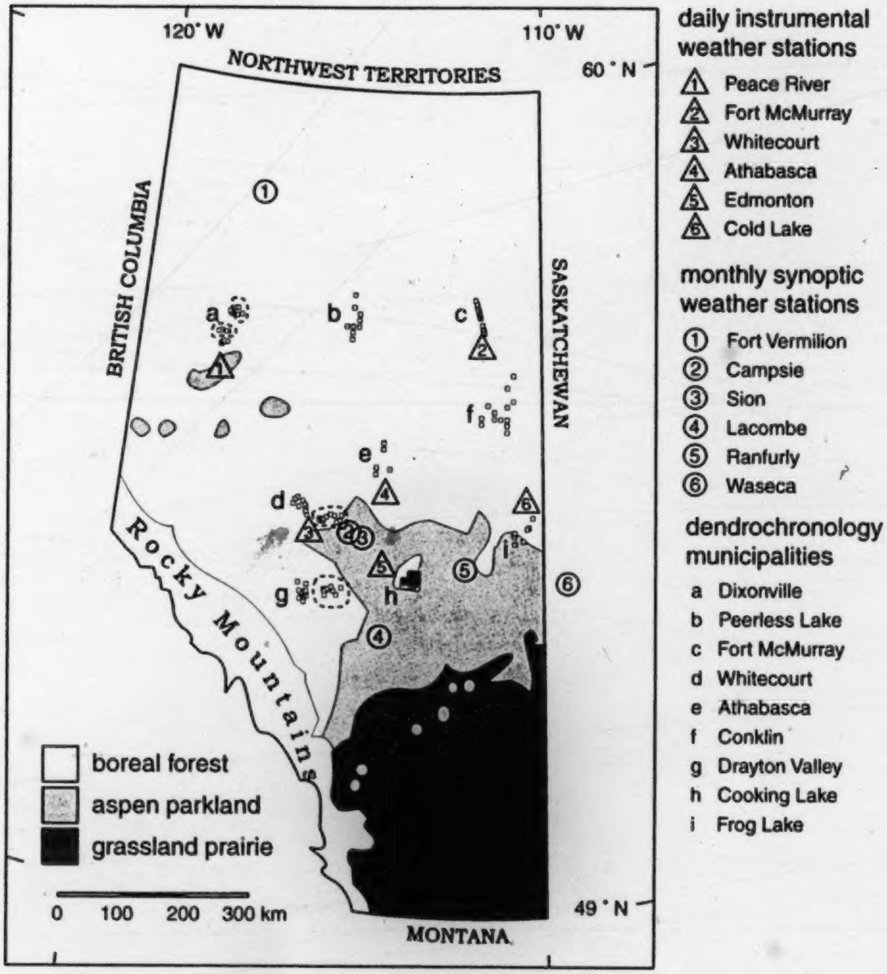
120° W
110° W
60° N
49° N
NORTHWEST TERRITORIES
BRITISH COLUMBIA
SASKATCHEWAN
MONTANA
Rocky Mountains
a
b
c
d
e
f
g
h
i
boreal forest
aspen parkland
grassland prairie
0 100 200 300 km
daily instrumental weather stations
1 Peace River
2 Fort McMurray
3 Whitecourt
4 Athabasca
5 Edmonton
6 Cold Lake
monthly synoptic weather stations
① Fort Vermilion
② Campsie
③ Sion
④ Lacombe
⑤ Ranfurly
⑥ Waseca
dendrochronology municipalities
a Dixonville
b Peerless Lake
c Fort McMurray
d Whitecourt
e Athabasca
f Conklin
g Drayton Valley
h Cooking Lake
i Frog Lake

Figure 3.1. Weather stations and aspen stands (squares) sampled in nine municipalities, (a) to (i), in northcentral Alberta. Dotted lines indicate clusters of plots located in fragmented forest. Forest regions redrawn from "Forest Regions of Canada" (Canadian Ministry of Supply and Services 1992, ISBN 0-662-97746-7).

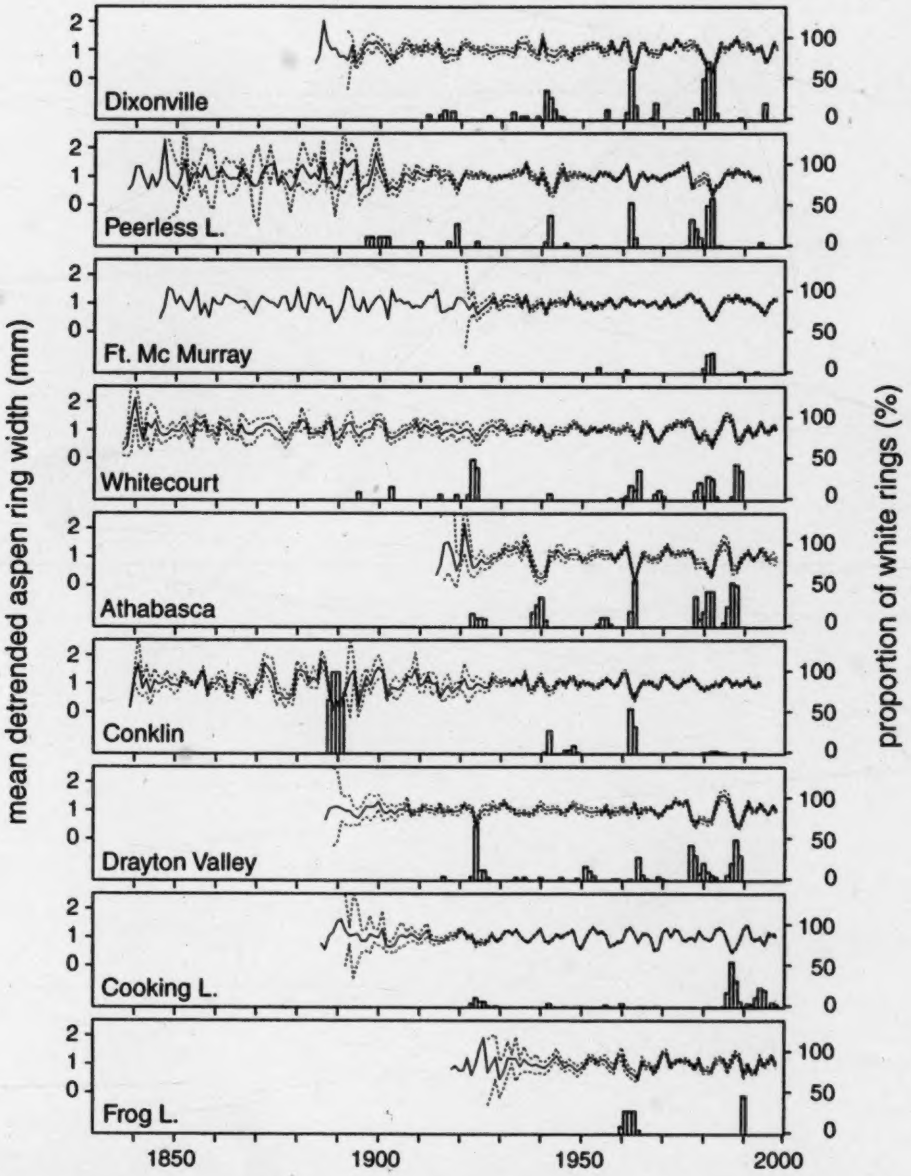

Figure 3.2. Aspen ring width chronologies for municipalities of Fig. 3.1. Solid lines indicate mean aspen ring width for a given year; dotted lines indicate 95% confidence interval. Bars indicate proportion of samples with white rings for a given year.

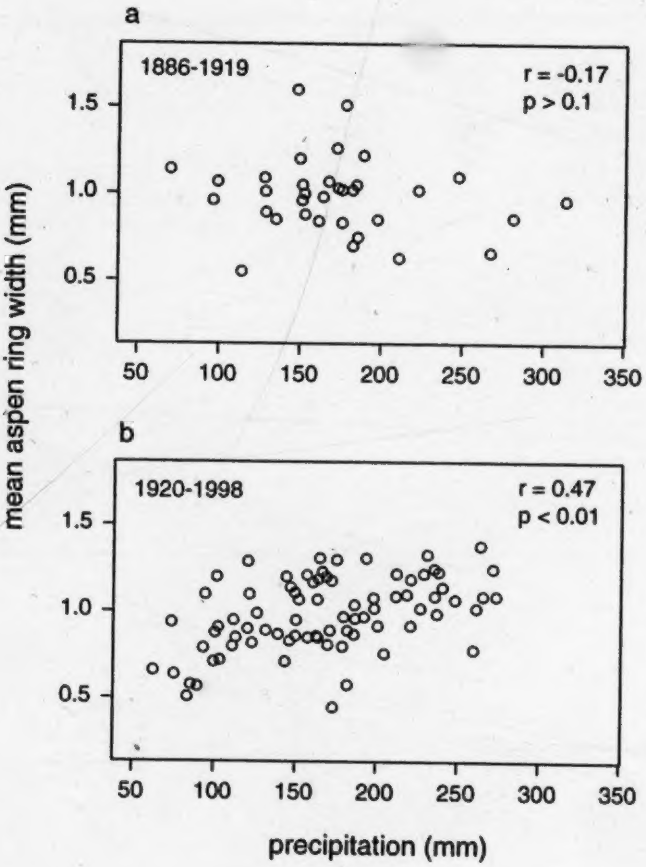

Figure 3.3. Correlation between March-June instrumental precipitation at Edmonton and mean detrended aspen ring widths over Cooking Lake municipal grid. (a) 1886-1919; (b) 1920-1998.

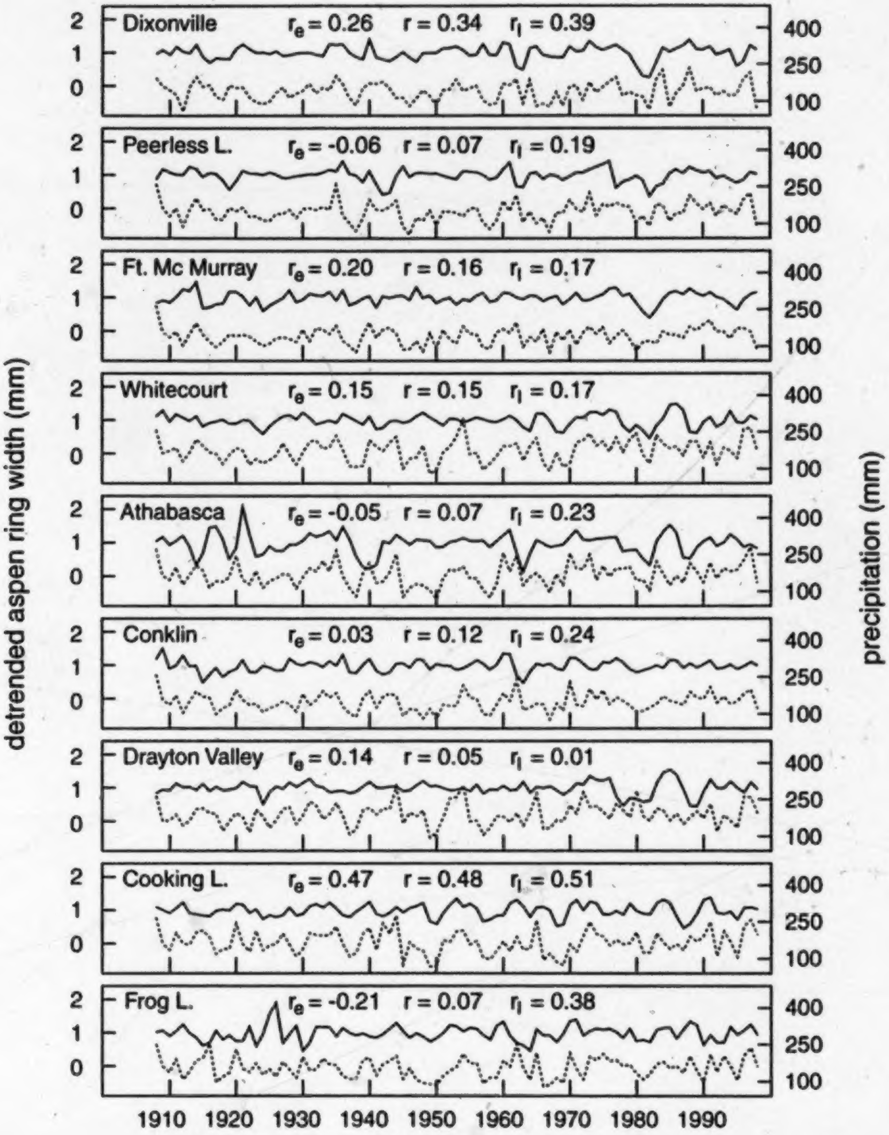

Figure 3.4. Correlation between annual fluctuations in detrended aspen ring widths and kriged estimates of March-June precipitation. Symbols r_e , r_l , r denote correlations over the periods 1908-1953, 1953-1998 and 1908-1998, respectively.

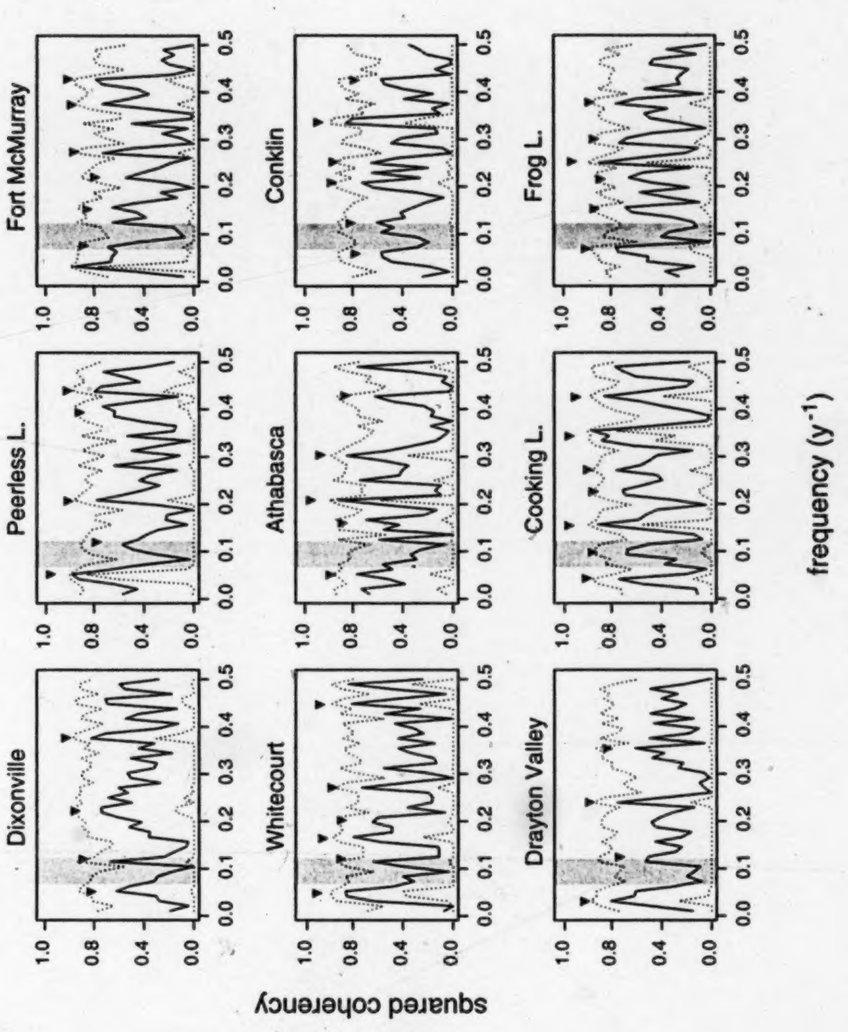

Figure 3.5. Cross-spectral coherency between aspen ring widths and kriged precipitation from 1908 to 1998 at each municipality. Dotted lines indicate 95% confidence intervals on coherency estimates. Arrows indicate dominant spectral peaks. Black arrows denote peaks near 20, 9.1, 6.5, 4.5, 3.7, 2.7 y. Note troughs in shaded decadal frequency range, except at Cooking Lake.

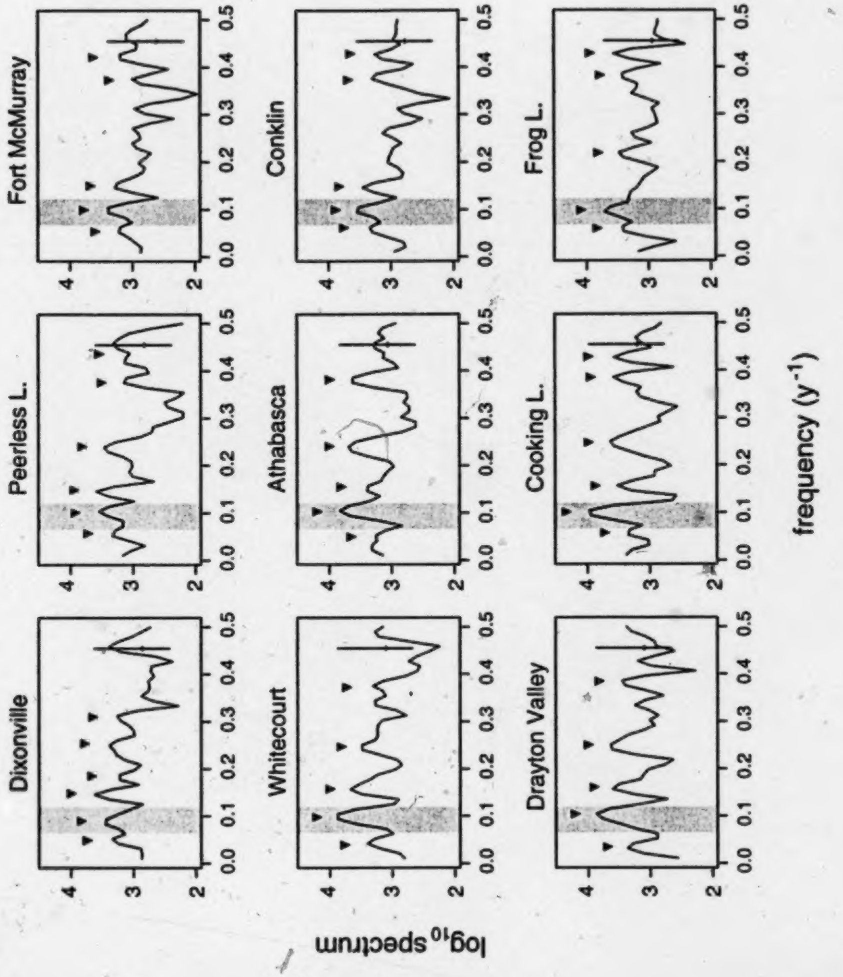

Figure 3.6. Spectrum of kriged precipitation 1908-1998 at each municipality. Horizontal and vertical lines indicate bandwidth and 95% confidence interval assuming white null spectrum. Spectra smoothed by Daniell smoother with spans={3}. Black arrows indicate dominant spectral peaks located near 20, 10, 6.5, 4.0, 2.7, 2.3 y. Note peaks in shaded decadal frequency range.

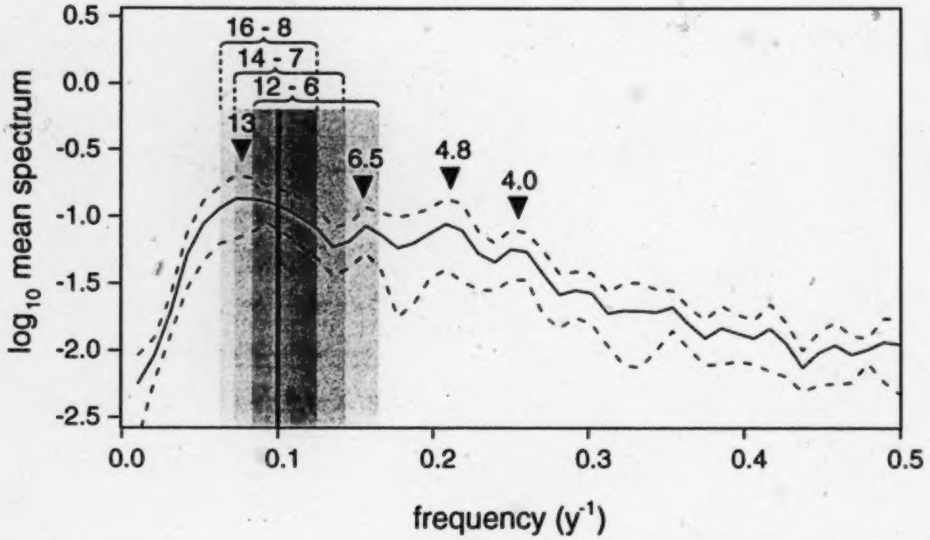

Figure 3.7. Average of smoothed spectra for detrended municipal aspen ring width chronologies 1908-1998, shown in Fig. 3.8. Dashed lines indicate 95% confidence intervals on spectral density estimates. Arrows indicate dominant frequencies. Peaks at 13 and 6.5 y are harmonics. Integral harmonic intervals within the range [6,16] are shown as shaded regions for comparative purposes. The interval [6,16] is commonly cited as the range in forest tent caterpillar outbreak periodicity (Hildahl& Reeks 1960, Witter 1979). The dark band marking 10 y indicates the estimated mean periodicity of forest tent caterpillar outbreaks (Baird 1917, Hodson 1941, Sippell 1962).

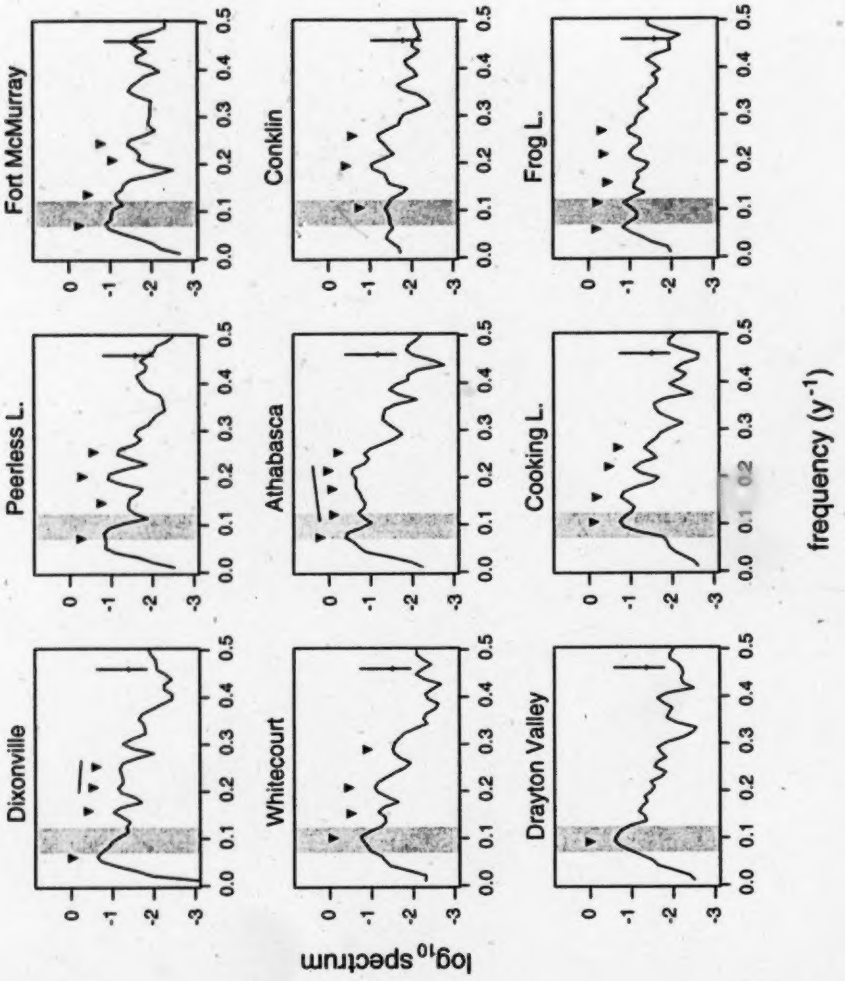

Figure 3.8. Spectrum of detrended aspen ring widths 1908-1998 for each municipal chronology. Horizontal and vertical lines indicate bandwidth and 95% confidence interval assuming white null spectrum. Spectrum smoothed by Daniell smoother with spans={3}. Arrows indicate dominant frequencies near 20, 10, 6.5, 5.8, 4.0 y. Note variation in precise location of decadal peak with respect to shaded region.

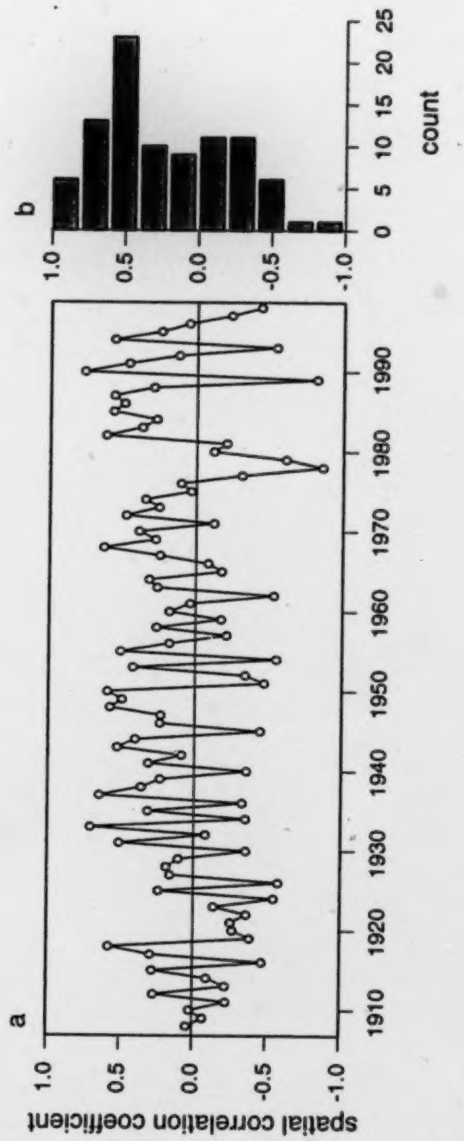

Figure 3.9. Annual fluctuation in spatial correlation between mean aspen ring width and precipitation over the nine municipalities of the provincial grid (a). Histogram in (b) shows correlation coefficient is bimodally distributed.

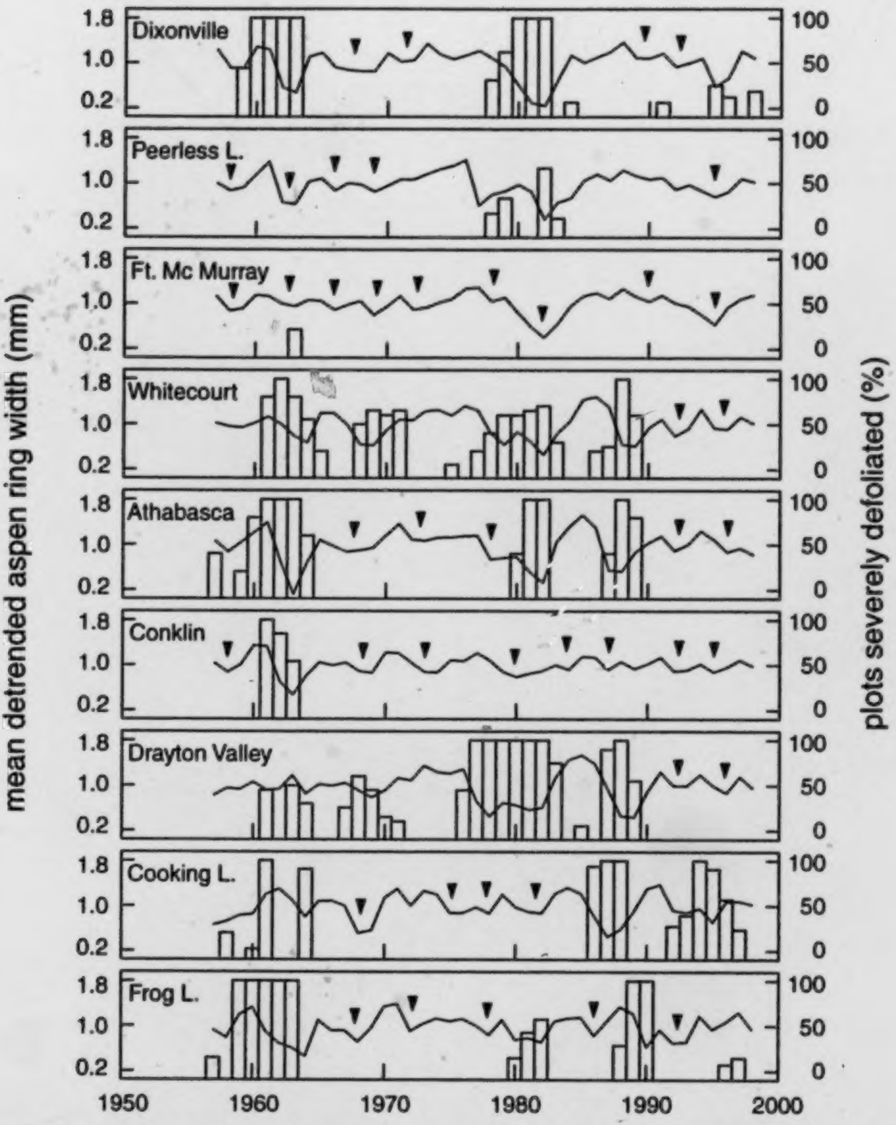

Figure 3.10. Temporal coincidence between aspen ring width (solid line) and extent of defoliation (bars) in each of the municipalities. Arrows indicate minor dips in growth in years where no defoliation was recorded in the municipality, but some defoliation was recorded in at least one of the other municipalities.

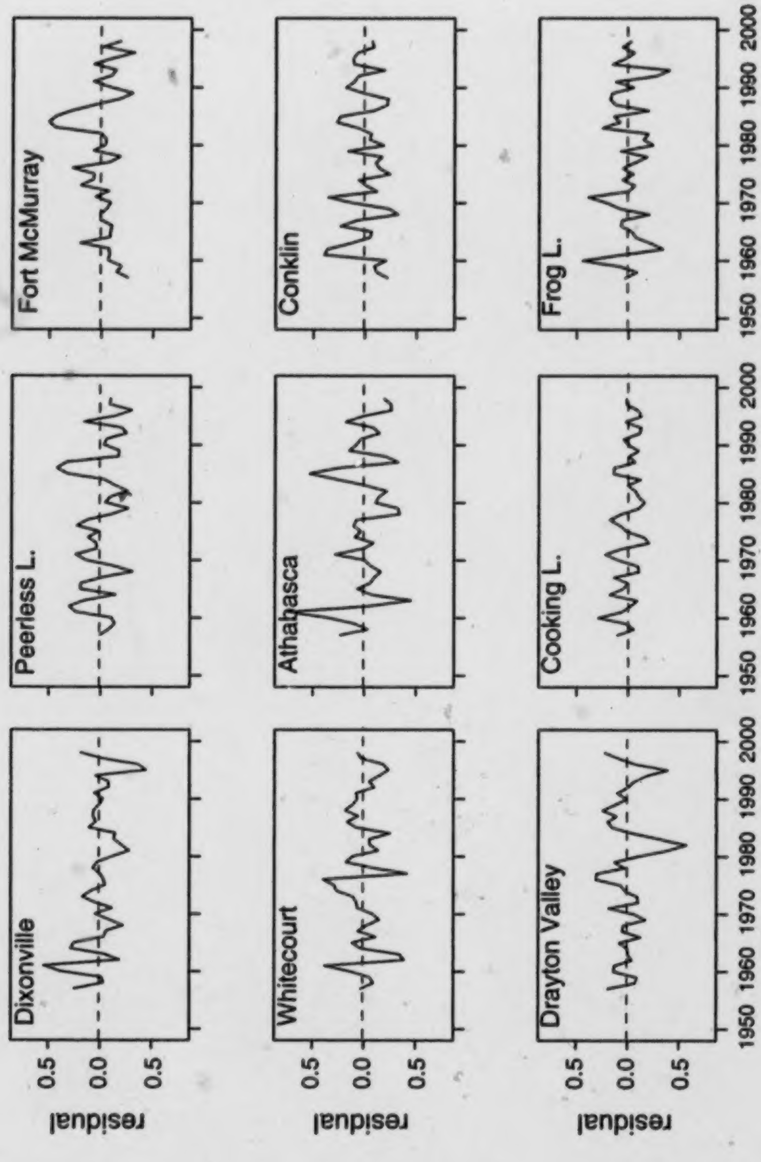

Figure 3.11. Residual aspen ring width from each municipal AR(0) defoliation model.

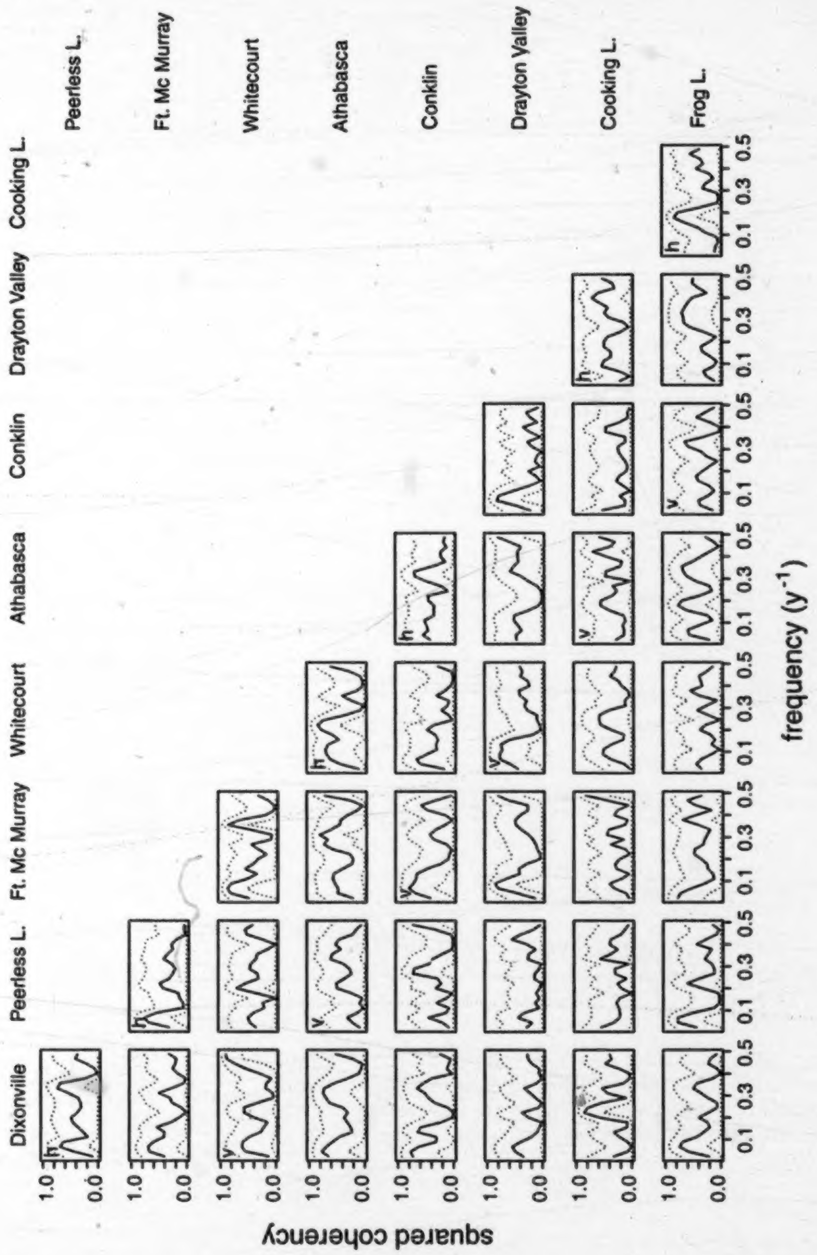

Figure 3.12. Cross-spectral coherence among residual aspen ring widths in Fig. 3.11. Symbols "h" and "v" indicate where municipalities are horizontal or vertical neighbours.

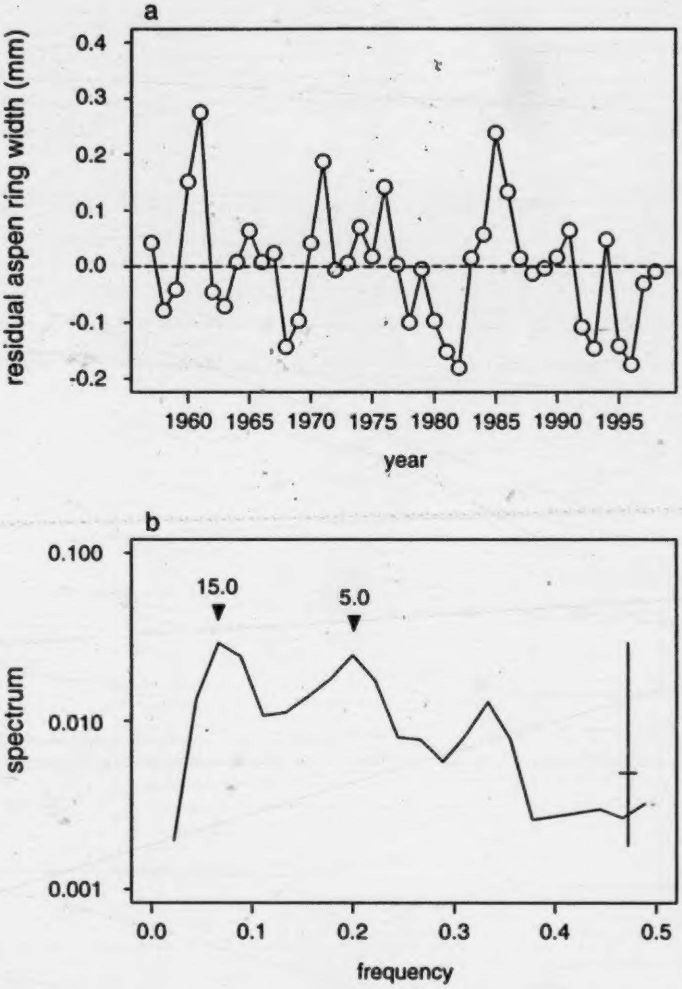

Figure 3.13. Residual aspen ring width from Fig. 3.11 averaged over the nine municipalities, and plotted in the (a) temporal and (b) frequency domains. Spectrum smoothed by Daniell smoother with spans={3}. Horizontal and vertical lines indicate bandwidth and 95% confidence interval, assuming white null spectrum.

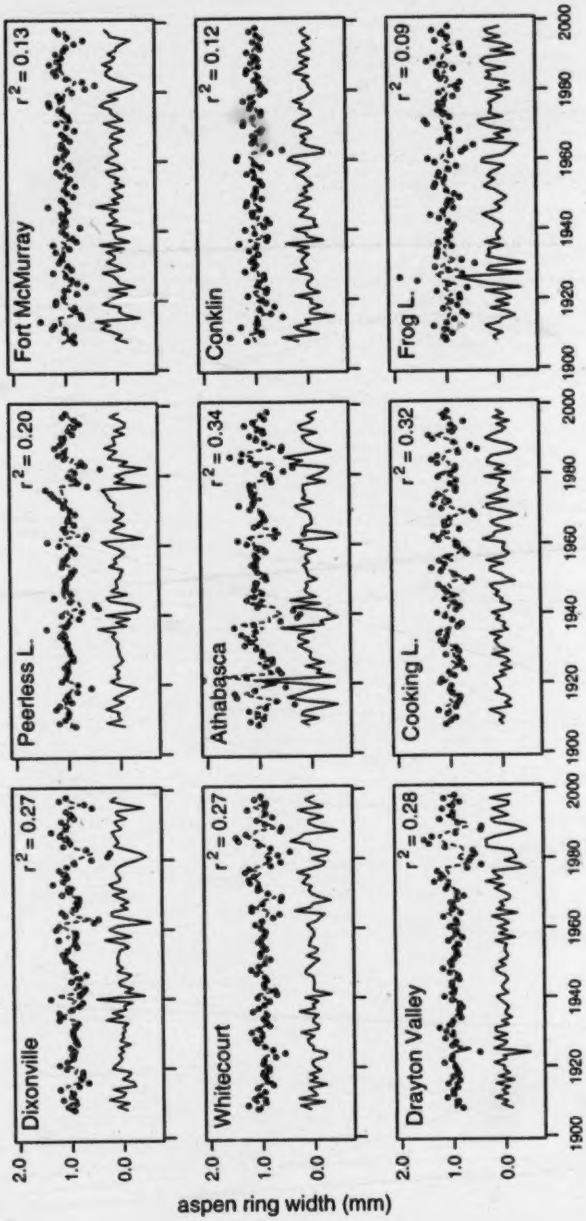

Figure 3.14. Aspen ring widths 1908-1998. Circles are original data. Dashed and solid lines represent fitted values and residuals from an ARMA(1,1) model.

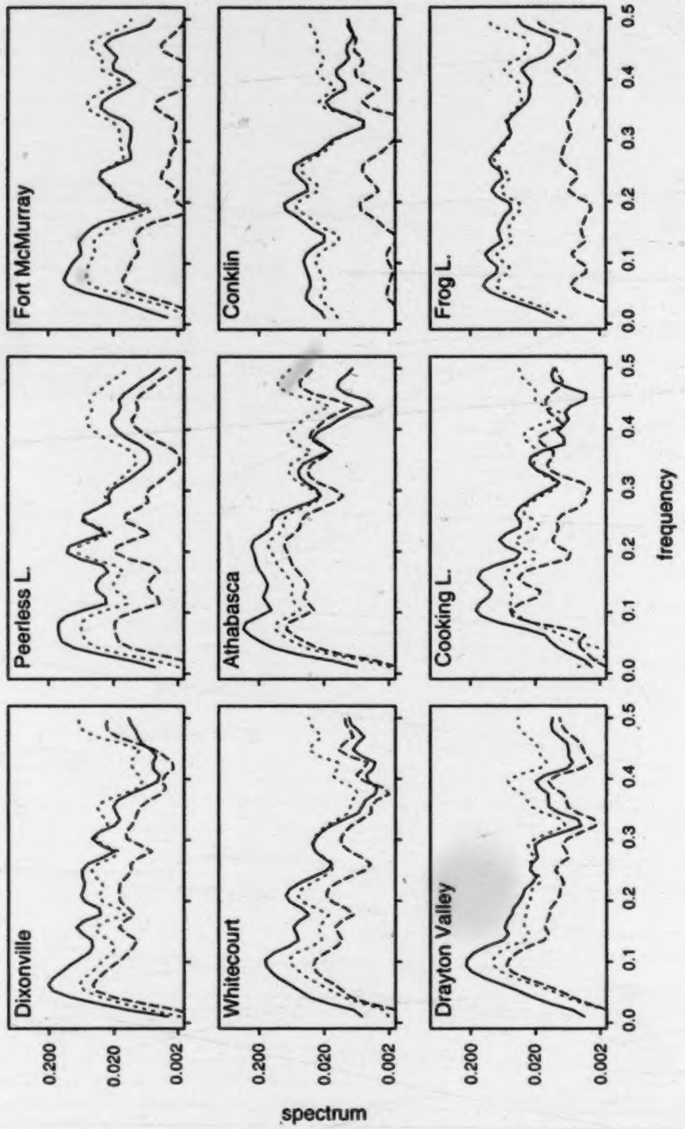

Figure 3.15. Spectra of aspen ring widths in Figure 3.14. Solid, dashed, and dotted lines represent original data, values fitted with an ARMA(1,1) model, and residuals. Spectra smoothed using spans of {3,3}.

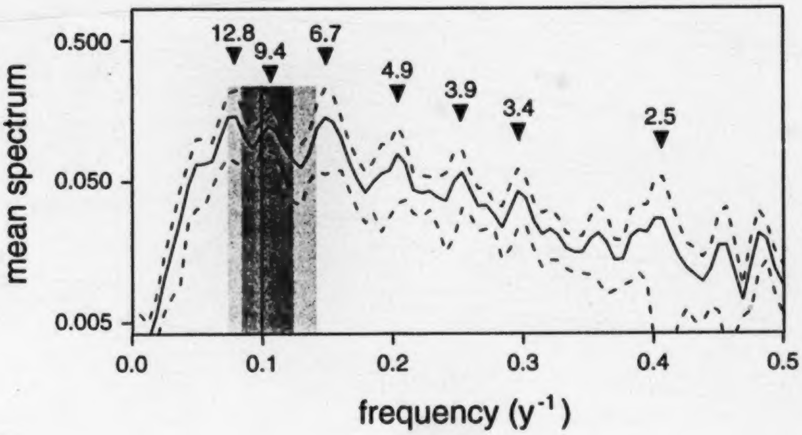

Figure 3.16. Average spectrum for the nine municipal aspen ring width chronologies 1837-1998. Before averaging, municipal spectra were pre-smoothed with a Daniell smoother using spans={3}. Dashed lines indicate 95% confidence intervals. Triangles denote dominant spectral peaks. Shaded regions indicate integral harmonic periodic intervals in the range [6,16] years, as in Fig. 3.7.

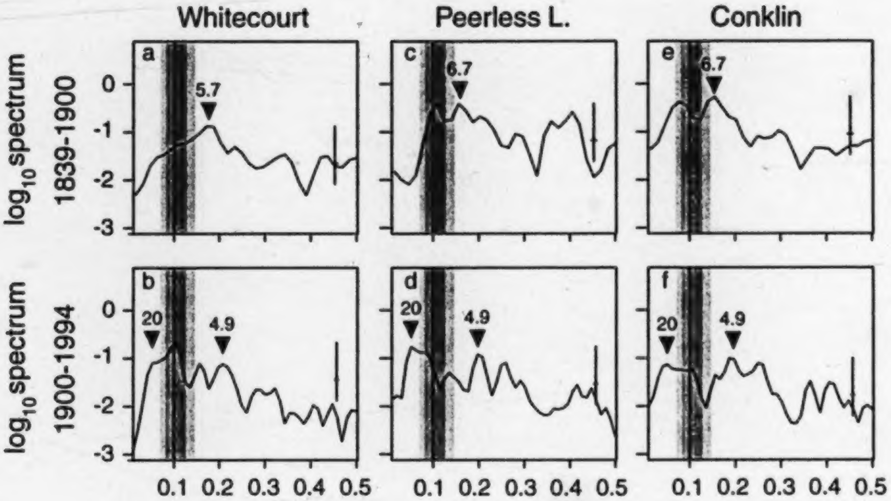

Figure 3.17. Spectra of detrended aspen ring width chronologies for (a) Whitecourt 1839-1900, (b) Whitecourt 1900-1994, (c) Peerless L. 1839-1900, (d) Peerless L. 1900-1994, (e) Conklin 1839-1900, (f) Conklin 1900-1994. Spectra smoothed by Daniell smoother with spans={3}. Horizontal and vertical lines on periodograms indicate bandwidth and 95% confidence interval, assuming white null spectrum. Triangles indicate dominant spectral peaks and shoulders outside the decadal range. Shaded regions indicate integral harmonic periodic intervals in the range [6,16] years.

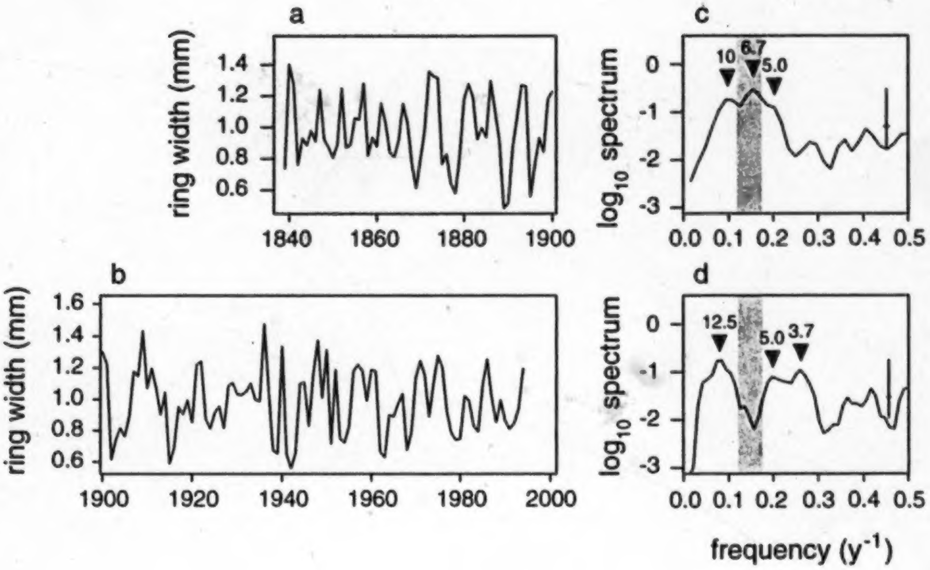

Figure 3.18. Mean of the three longest aspen ring width chronologies from the boreal region: (a) 1839-1900, (b) 1900-1994. Spectra in (c) and (d) smoothed by Daniell smoother with spans={3}. Horizontal and vertical lines on periodograms indicate bandwidth and 95% confidence interval, assuming white null spectrum. Triangles indicate dominant periodicities. Shaded region from 0.12 to 0.17 y^{-1} (8.3 to 5.9 y) emphasizes spectral differences between periods.

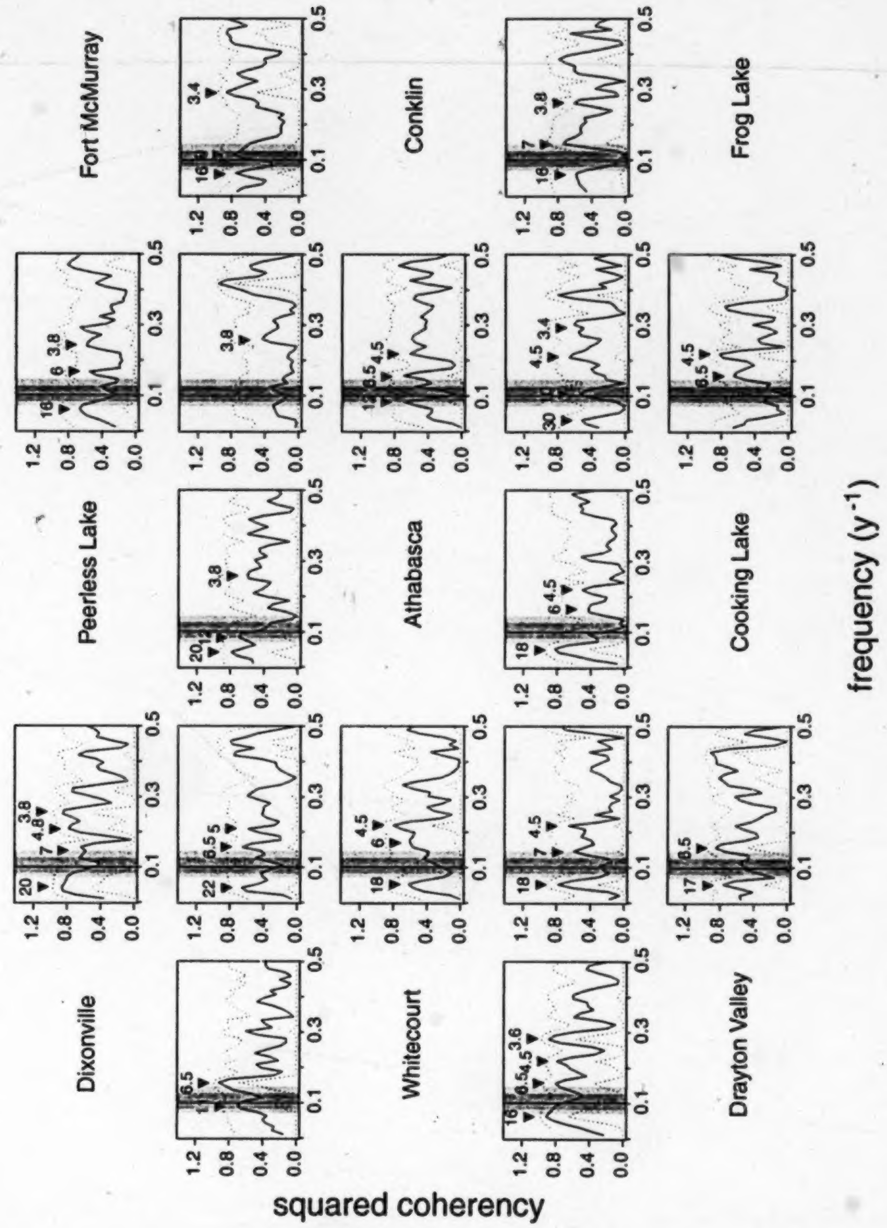

Figure 3.19. Cross-spectral coherence among climate-corrected aspen ring width chronologies from neighbouring pairs of municipalities. Symbols explained in Fig. 3.16.

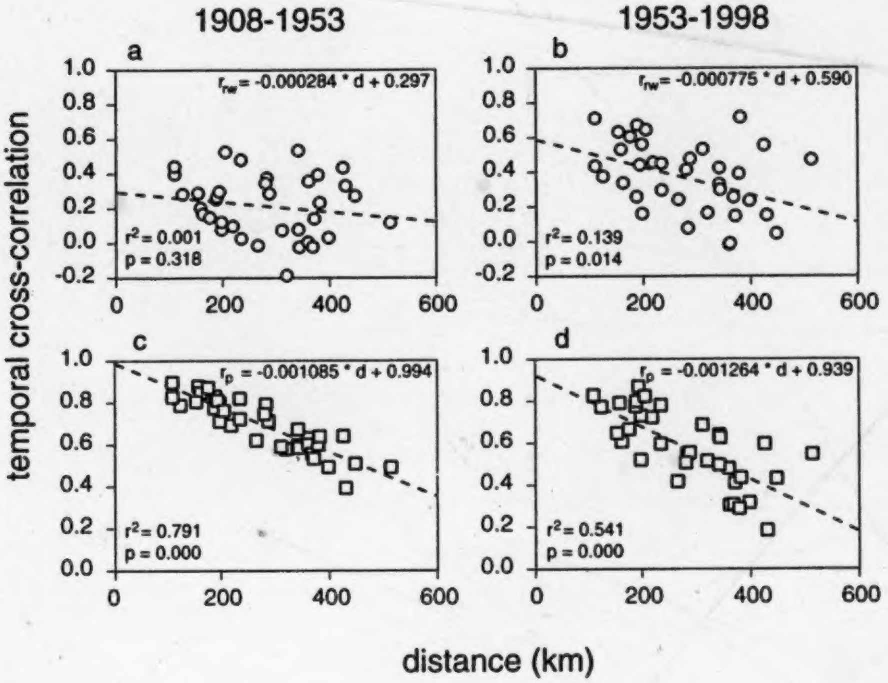

Figure 3.20. Distance-dependent synchrony decay in aspen growth (circles, top panels) and kriged estimates of March-June precipitation (squares, bottom panels) during 1908-1953 (left panels) and 1953-1998 (right panels) among municipalities. Data points represent temporal cross-correlation between pairs of municipalities, which are separated by a certain variable distance. In regression equations, r_{rw}, r_p, and d refer to cross-correlation in aspen ring width, cross-correlation in precipitation, and distance.

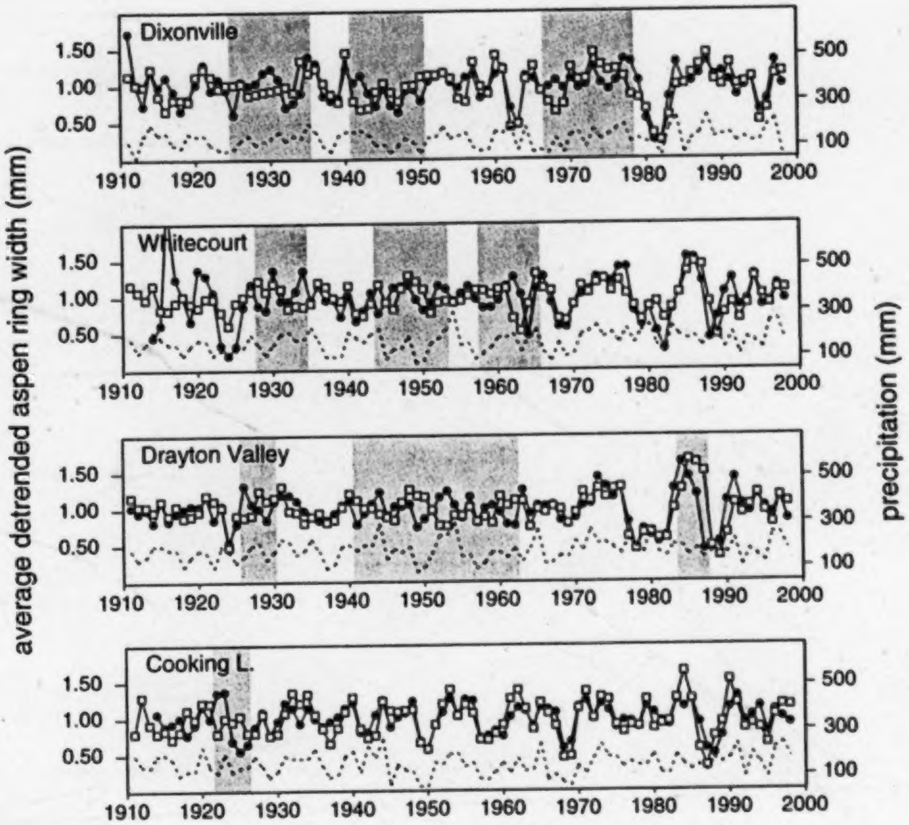

Figure 3.21. Uncorrected aspen ring widths for chronologies assembled from clusters of continuously forested (▫) and fragmented (•) stands at each of four municipalities. Dashed line is kriged estimate of March-June precipitation. Shaded regions indicate periods of disturbance asynchrony among clusters within each municipality.

4. SURVIVORSHIP BIAS IN DENDROECOLOGICAL RECONSTRUCTION OF FOREST TENT CATERPILLAR OUTBREAKS USING TREMBLING ASPEN

4.1 Introduction

It is well understood that dendrochronological records from living trees provide a biased sample of historical events. As time passes, some stems die while others survive. Dendrochronological history is therefore written by the survivors, and this historical account may be biased by survivorship.

Survivorship does not influence the qualitative pattern of annual fluctuations in annual ring widths and it is therefore not a concern to the dendrochronologist interested in cross-dating tree rings. But survivorship does modulate annual ring widths in surviving trees. As trees are lost from a stand, the statistical distribution of ring widths in surviving stems will vary; apparent growth rates for some years will be inflated while others will be deflated. If survivors are selected randomly, then inflationary and deflationary selection events tend to balance one another and survivorship bias is neutral. If selection is non-random, however, survivorship bias may not be neutral and the statistical distribution of ring widths may drift as trees are lost from a stand over time. For example, if trees with low growth rates are more vulnerable to mortality, survivorship bias would tend to inflate apparent over-all growth rates.

Survivorship bias can be a serious concern to dendroclimatologists and dendroecologists who use tree ring widths to inferentially reconstruct past climatic and disturbance regimes. If the only effect of survivorship bias is to modulate the mean or variance of annual ring widths, then, in theory, it is a simple matter to correct for such bias. The effects, however, can be more insidious. For example, if a large-scale disturbance, such as drought or pathogenic invasion, leads to both reduced growth rates and increased mortality, then survivorship bias will influence the autocorrelation structure in annual ring width chronologies. In such a case the precise impact of survivorship bias on inferred history is more difficult to quantify.

The problem of survivorship bias in dendroecological reconstruction is especially relevant where pulses of reduced growth are concomitant with pulses of mortality, as in an insect outbreak. If insect defoliation tends to kill trees without affecting growth, then no record of defoliation would be made in the annual rings of surviving trees. In contrast, if defoliation rarely kills trees, then even after many outbreaks, historical impacts would persist in surviving stems in the form of narrow rings. Here defoliation would act merely as a stem growth perturbation, much like drought, and dendroecological inferencing of past defoliation may be accomplished much as dendroclimatological reconstruction of past climatic fluctuations. Thus in order to infer past insect defoliation from tree ring widths it is important to know how the detectability of past insect defoliation in annual growth fluctuations is compromised by differential stem mortality resulting from the cumulative effect of subsequent disturbances.

Throughout central North America, populations of the forest tent caterpillar (*Malacosoma disstria* [Hbn.]) periodically erupt and cause widespread defoliation of trembling aspen (*Populus tremuloides* Michx.) (Hildahl & Reeks 1960, Sippell 1962, Ives 1973, Hodson 1977, Hogg 1999). Local infestations tend to persist for two to three years (Churchill *et. al.* 1964) while regional outbreaks may persist longer.

Cross-sections of aspen stems reveal the impact of severe and sustained defoliation as a series of narrow rings that are often whitish in hue when finely sanded (Hogg & Schwarz 1999). Annual growth rates are often reduced by as much as 70-90% (Duncan & Hodson 1958, Hogg 1999), suggesting the forest tent caterpillar is an important factor affecting aspen growth. Severely defoliated trees often exhibit crown necrosis and subsequent secondary infections by various pathogens and wood-boring beetles (Duncan & Hodson 1958, Hildahl & Reeks 1960, Churchill *et. al.* 1964).

If defoliation by forest tent caterpillar increases the probability of aspen mortality, then samples acquired after an outbreak should exhibit a maximal impact response and samples acquired many decades later should exhibit a lesser response. This would cause a problem for dendroecological reconstruction of outbreaks. Suppose a ring width chronology exhibited a sustained reduction in growth in the early portion of the chronology and a larger growth reduction later in the chronology. If both disturbances were due to tent caterpillar defoliation, then, without knowing the differential rate of mortality among defoliated and non-defoliated trees, one can not be sure that the apparent differences in growth reduction are due to a real difference in outbreak magnitude.

In aspen, it seems forest tent caterpillar outbreaks are not a direct, immediate cause of tree mortality (Ghent 1958, Duncan & Hodson 1958, Hildahl & Reeks 1960, Churchill *et. al.* 1964). Thus it should be possible to infer past outbreaks from aspen ring widths. The critical questions are: (1) how far back in time can one assume that survivorship bias is negligible? (2) how can this bias be corrected such that dendroecological reconstructions will be temporally homogeneous? This study addresses the first question, whether the impacts of a forest tent caterpillar outbreak on aspen growth are as detectable 40-50 years after outbreak as they were the first year after outbreak.

4.2 Methods

4.2.1 Historical chronologies

A large portion of northern Minnesota, including Kabetogama State Forest and Cloquet Valley State Forest (Fig. 1), had been sampled in 1955 to estimate the impact on aspen growth of a 1951-1954 outbreak of forest tent caterpillar. Based on whether plots experienced severe defoliation in either 1952, 1953, or both years, three chronologies covering the years 1950-1954 were assembled (Froelich *et. al.* 1955). These confirm that defoliation began in the north and spread south and east, such that the "1952 outbreak" chronology largely reflected the progression of defoliation around International Falls, and the "1953 outbreak" chronology reflected the progression of defoliation around Duluth.

This outbreak also affected parts of Saskatchewan, Canada. To estimate the local impacts of this outbreak, aspen samples had been taken in 1957 from plots located at Doré L. and Big River, located 100 km northwest and 50 km west of Prince Albert National Park, which is 100 km north of Prince Albert (Fig. 1). These had been used to develop ring width chronologies covering the period 1946-1956 (Hildahl & Reeks 1960).

4.2.2 Modern sampling

Aspen stands in the Kabetogama State Forest and the Cloquet Valley State Forest (Minnesota) were re-sampled in July 2000 to determine if the impact of the 1951-1954 outbreak was as apparent as it was in the historical aspen ring width chronologies. Three plots, each containing a single tree, were located in each the two forests. Basal sections from each of the six aspen stems were taken at 1.3 m above ground. These were air-dried and sanded to 400 grit using an orbital hand-held sander. Ring widths were measured to 0.08 mm accuracy using an ocular micrometer on a stereo dissecting microscope with magnification set to 12.5x.

Eight aspen stems from Prince Albert National Park (Saskatchewan) were sectioned in 1995 and processed in a similar manner. These samples could be compared to a 1957 sample of two and four trees taken from Doré L. and Big River. Due to the large distance between plots at Doré L., Big River and Prince Albert National Park and natural spatiotemporal variation in tent caterpillar outbreak patterns at that scale (Cooke & Roland 2000), we suspected *a priori* that stand-level defoliation histories might differ between these areas. To maximize the chance of obtaining a fair comparison, the Doré L. and Big River historical chronologies were not pooled but compared separately to the modern Prince Albert National Park chronology.

4.2.3 Statistical analysis

Individual stem chronologies showed no obvious growth trends so annual ring widths were simply averaged among samples to create mean chronologies. The modern chronologies from Minnesota were compared graphically to historical forest tent caterpillar census data and defoliation maps (Hodson 1977) for the period 1948-1959 to confirm that forest tent caterpillar was the cause of growth reduction.

Each modern chronology was compared with the appropriate historical chronology to determine if the ring width profiles differed among sampling times. For each year in the chronology, Student's *t*-test was used to compare annual relative growth rates of modern and historical samples. The annual relative growth rate was computed as the annual ring width divided by the stem radius. By using relative growth rates, differences among stems in mean growth rates were factored out of the analysis. Consequently, the tests were comparing annual departures from normal growth.

As individual stem data were not available for the Minnesota historical chronologies, a one-sample *t*-test was used to compare annual relative growth rates from each modern chronology to the mean annual relative growth rates from the appropriate historical mean chronology, for each year from 1950 to 1954. Individual stem data were available for the Saskatchewan historical chronologies, so a two-sample *t*-test was used to compare annual relative growth rates from the modern chronology to those from each of the two historical chronologies, for each year from 1946 to 1956. All analyses were conducted with Minitab (Minitab Inc., State College, PA).

4.3 Results

The Kabetogama and Cloquet Valley aspen ring width chronologies agreed well with both the Minnesota defoliation maps and the forest tent caterpillar census data of Hodson (1977, his Figures 1-20): an outbreak of forest tent caterpillars began in the north in 1951 and spread southward, lingering in the Cloquet Valley locality for several years before collapsing suddenly in 1959 (Fig. 2). The aspen ring width chronologies revealed additional disturbances in 1968-1973, 1977-1981 and 1988-1992 (arrows in Fig. 2). As with the 1951-1959 disturbance, these were not perfectly synchronized between sites. These disturbances were caused mostly by forest tent caterpillar defoliation, with some contribution by the large aspen tortrix (*Choristoneura conflictana* [Walker]), as revealed by aerial survey maps (Beach 1968, 1969, 1970, 1971a, 1971b, 1971c, Minnesota Dept. Nat. Resources 1974, 1975, 1976, 1977, 1978, Minnesota Dept. Nat. Resources Div. of Forestry 1979, 1980, 1981, 1989, 1990, 1991). Severe defoliation was evident in 2000 as well in plots where stem sections were collected for this study. Notably these coincided with large-scale outbreaks in northwestern Ontario, Canada (Daniel & Myers 1995), which borders Minnesota to the north (Fig. 1).

The severe 1952 and 1953 outbreak impact revealed in 1955 samples was also evident in modern samples (Fig. 3). Even after three additional outbreaks, the 1950-1954 dip in the ring width profiles of the modern samples was just as severe as it appeared to be in the historical chronology. If anything, growth impacts at Kabetogama in 1951 and Cloquet Valley in 1953 and 1954 seemed more severe in the modern samples than in the historical chronologies.

These results were roughly mirrored in the Saskatchewan comparison between modern and historical samples, although growth disturbances in 1951 and 1952 at Big River and in 1953 at Doré L. were more severe than those revealed in modern samples (Fig. 4). Interestingly, the Prince Albert National Park modern chronology more closely resembled the Doré L. historical chronology than the Big River historical chronology, yet Doré L. is more than twice as far away (Fig. 1).

4.4 Discussion

The Minnesota data show no evidence of survivorship bias. The slightly lower growth rate for 1951 found in modern samples is probably a result of slightly different stand defoliation histories. Froelich *et. al.* (1955) separated their aspen stands into three groups based on whether severe defoliation occurred in 1952, 1953 or both years. Had they created a fourth category for stands defoliated more in 1951 than either 1952 or 1953, the resulting ring width chronology might have resembled that of Kabetogama State Forest. This would underscore the importance of re-sampling as near as possible to the original plot locations.

The Saskatchewan data are less easily interpreted. The small dip in growth in 1953 at Prince Albert National Park was associated with a more severe dip in 1953 at Doré L. and a more prolonged dip from 1951-1953 at Big River. Thus it seems likely that all stands were defoliated to some extent by forest tent caterpillar. The lack of a sustained dip from 1951 to 1953 in the modern ring width chronology might be taken as evidence that survivorship bias in modern samples reduced the detectability of that outbreak. For example, it might be postulated that the 1953 dip in the modern chronology is all that remains of the evidence of the outbreak that was so easily inferred from 1957 samples. A different interpretation, however, seems more plausible.

Differences between historical and modern chronologies in Saskatchewan are likely a result of the spatial distance between sampled plots. In other words, it is likely that Prince Alberta National Park, Big River and Doré L. are far enough apart that each experienced different defoliation histories. For example, variation in the pattern of reduced growth from 1951 to 1953 might have resulted from imperfectly synchronized outbreaks (Hildahl & Reeks 1960). Support for this view lies in the similarly quasi-synchronous defoliation events noted in the Minnesota data.

Notably, the 1946 growth disturbance was stronger in modern samples than in historical samples. If the 1946 dip was caused by forest tent caterpillar defoliation, this would refute the survivorship bias hypothesis. However, in all Saskatchewan chronologies, the 1946 dip occurred suddenly and was not sustained through to 1947, suggesting it was probably not due to insect defoliation, but to an instantaneous meteorological perturbation such as the heavy snow which fell on May 9 after an extended warm period in late April (Environment Canada, unpublished data). Such events are infrequent on the Canadian Prairies, but they do occur in both late spring and early autumn and they are known to cause widespread crown damage (Gill 1974) and to reduce aspen growth rates over several hundred square kilometres (chapter eight). This substantial spatial variation in perturbation severity corroborates the view that historical and modern sampling plots were too far apart to experience precisely the same regime of disturbance.

Our results support the view that forest tent caterpillar outbreaks do not substantially accentuate secondary mortality of overstorey stems. This is somewhat surprising given that *Hypoxylon*, *Nectria*, and wood-boring beetles (*e.g. Saperda*) occur more frequently on aspen stems weakened by severe and prolonged defoliation (Churchill *et. al.* 1964). Perhaps the vast majority of stems are insufficiently defoliated to evoke a strong secondary attack. The low variation in impact among stems within a stand is also surprising because early-season, between-stem variation in caterpillar density is often quite high due to the colonial feeding habit of young larvae (Batzer *et. al.* 1995). One hypothesis is that clonal aspen may buffer nutritional stresses by pooling resources among stems through inter-connected root systems. In this manner, the impact of defoliation might be shared among trees within a clone.

Although the number of modern samples was quite small, more intensive sampling of stands would probably not alter the chronologies substantially because the impact of an outbreak is surprisingly homogenous within clonal stands (chapter two). We were not able to sample the exact stands used by Froelich *et. al.* (1955) and Hildahl & Reeks (1960) so there may be a difference in sampling bias. For example, there is a possibility that our sample stems in Minnesota happened by chance to be located in stands more vulnerable to tent caterpillar attack. More extensive sampling of stands would help clarify this issue. Similarly, closer geographic matching of plots in Saskatchewan would help make this data set more comparable the Minnesota scenario.

It is not known whether survivorship bias becomes significant after, say, 100 or 150 years, but this is a possibility. The issue of survivorship bias could be clarified further by collecting modern samples from Black Sturgeon L. (Ontario, Canada) and comparing these chronologies to aspen ring width data presented by Ghent (1952) which extend as far back as 1865 and show clear outbreak impacts in 1882 and 1938. Aspen typically do not live much longer than 80 years; however trees twice this age have been found in California and the Rocky Mountains (Perala 1991) as well as the boreal forest of Alberta (chapter three). Extensive sampling might be required to locate living trees older than 120 years. On the other hand, dendroecological outbreak reconstruction can be carried out using much older, rotten wood (Ghent 1958) using a method of paraffin impregnation (Ghent 1954).

A search of the literature suggests there are no other historical aspen chronologies available for comparison; however additional chronologies for other areas may exist as unpublished data or as unprocessed samples in storage. A universal constraint in such comparisons, however, is the difficulty in re-sampling the same stands that comprise the original chronologies.

4.5 Conclusion

After 45 years and three additional forest tent caterpillar outbreaks, the population of ring width profiles from aspen stems in Minnesota did not change despite substantial selection via stem mortality. Similar, albeit weaker, results were obtained in Saskatchewan.

If differential mortality of aspen stems is low enough to prevent the induction of strong survivorship bias, this simplifies the task of inferring the magnitude of past tent caterpillar outbreaks from an annual sequence of aspen ring widths because it implies that impacts deduced from the early part of a chronology are comparable to impacts deduced from the later parts of a chronology. Although survivorship bias seems to be negligible in the case of tent caterpillars on aspen, the same may not be true in other herbivore systems, such as spruce-spruce budworm. Here dendroecological reconstruction may be more precarious.

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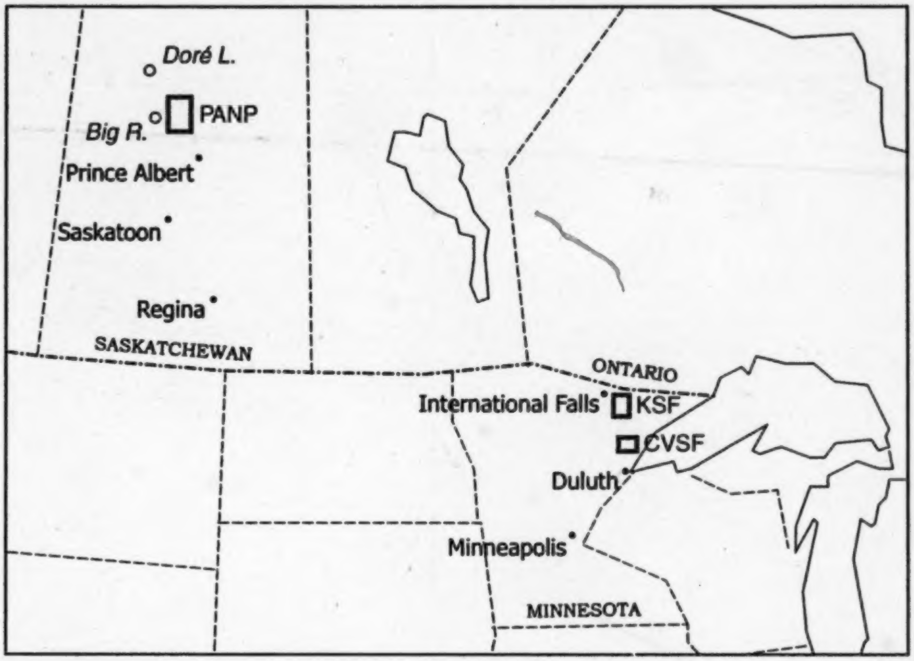
Doré L.
Big R.
PANP
Prince Albert
Saskatoon
Regina
SASKATCHEWAN
ONTARIO
International Falls
KSF
CVSF
Duluth
Minneapolis
MINNESOTA

Figure 4.1. General location of plots in Minnesota and Saskatchewan. Historical samples (1955) from Minnesota came from all over northern Minnesota (individual stem data unavailable, n=185). Modern samples (2000) from Minnesota came from Kabetogama State Forest (KSF, n=3) and Cloquet Valley State Forest (CVSF, n=3). Historical samples from Saskatchewan (1957) came from Big River (n=4) and Doré Lake (n=2). Modern samples (1995) from Saskatchewan came from Prince Albert National Park (PANP, n=8).

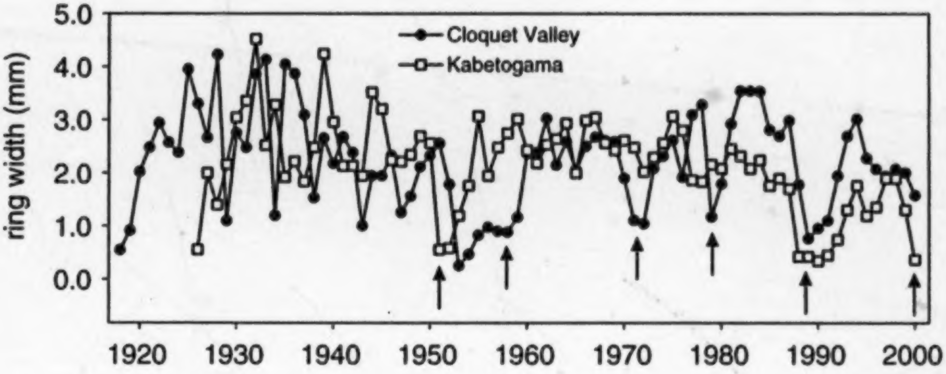

Figure 4.2. Mean aspen ring widths for Kabetogama State Forest (open squares) and Cloquet Valley State Forest (filled circles). Arrows indicate local outbreaks of forest tent caterpillar.

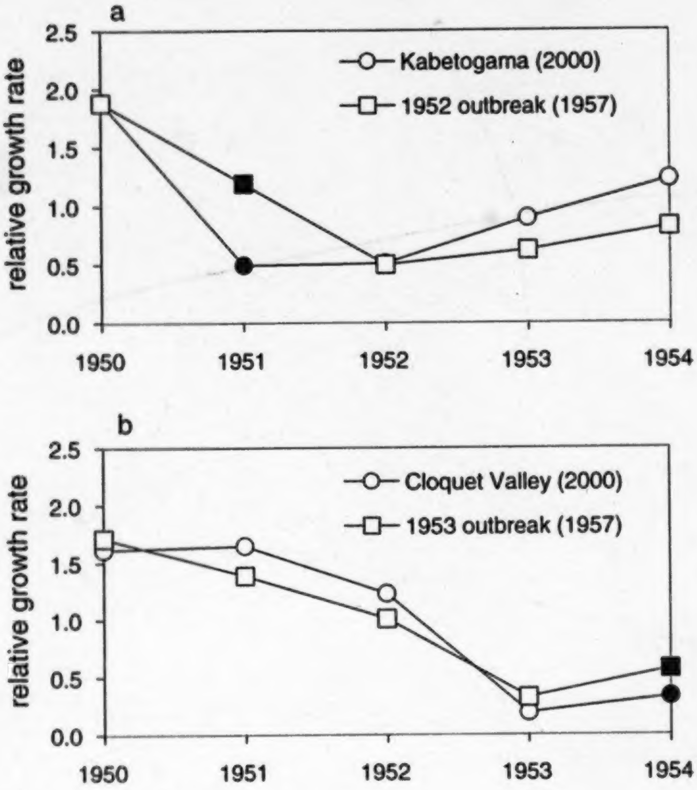

Figure 4.3. Aspen annual relative growth rates from modern (circle) and historical (square) chronologies from two parts of northern Minnesota: (a) Kabetogama State Forest modern chronology compared to historical chronology for plots defoliated in 1952 (Froelich *et. al.* 1955); (b) Cloquet Valley State Forest modern chronology compared to historical chronology for plots defoliated in 1953 (Froelich *et. al.* 1955). Filled symbols indicate years where relative growth rates differ significantly ($p<0.05$, one-sample *t*-test) between modern and historical chronologies.

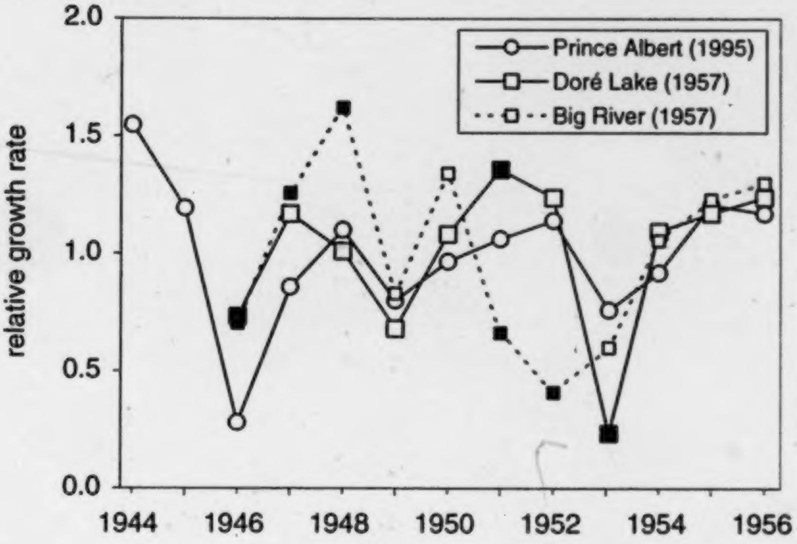

Figure 4.4. Aspen annual relative growth rates from modern (circle) and historical (square) chronologies from Prince Albert National Park, Doré Lake and Big River in central Saskatchewan. Filled symbols indicate years where ring widths differ significantly ($p<0.05$, two-sample *t*-test) between modern and historical estimates of mean aspen ring width.

5. ARE FOREST TENT CATERPILLAR OUTBREAKS CHAOTIC?

5.1 Introduction

5.1.1 Complex dynamics in natural populations

Understanding the nature of temporal fluctuations in animal populations has been a central theme in population ecology (Nicholson & Bailey 1935, Andrewartha & Birch 1954, Royama 1992). Much effort has been spent investigating the endogenous and exogenous regulatory mechanisms that could be responsible for the induction of low-frequency cyclicity or high-frequency variability, but progress has been slow. Particularly puzzling are the numerous cases where populations of forest insects appear to fluctuate neither randomly nor periodically (Turchin & Taylor 1992). A consensus is emerging that these systems are likely regulated by a combination of forces both endogenous and exogenous, such that fluctuations are not well explained by density nor any one environmental factor (Turchin 1995). Yet, despite widespread support for this general view, the very best insect pest population models (*e.g.* gypsy moth (Liebhold & Elkinton 1990, Liebhold & McManus 1991), spruce budworm (Royama 1984), mountain pine beetle (Berryman 1976)) are still inadequate.

5.1.2 Chaos in animal population ecology

Failure to predict future population behaviour has been attributed to numerous causes including a lack of understanding about the nature of regulation, the influence of environmental and demographic stochasticity, and non-stationarity of key environmental factors. But against this suite of possibilities lies the ever-present alternative hypothesis that population growth is an inherently chaotic process (May 1974). Here it is supposed that extreme sensitivity to small differences in population density prevents a population trajectory from ever settling onto a single, final course though phase-space. In the temporal domain, this leads to irregular, non-repeating patterns of population fluctuations which are impossible to predict in the long-term, but which are nonetheless bounded from below and above. According to this scheme, the influence of stochasticity is negligible, and chaotic irregularity is entirely deterministic in origin.

Deterministic non-periodic behaviour was first reported by Lorenz (1963) in a mathematical analysis of a meteorological simulation model comprising a set of three ordinary differential equations. May (1974, 1976) was the first to study chaos resulting from highly nonlinear density-dependent recruitment in theoretical ecological models. Many ecologists recognized the potential importance of chaos in accounting for previously inexplicable variability, but progress in the empirical domain was hindered by the lack of suitable methods for detecting chaos in real data, particularly regarding univariate time-series.

Schaffer & Kot (1985) finally broke through that barrier by applying Takens (1981) theorem to several classic ecological data sets, including the cases of measles in humans, Canadian lynx, and *Thrips*. Suggesting that these systems were governed by chaotic "strange attractors", they sparked renewed interest in the study of chaos, and challenged ecologists to prove otherwise. Their work was criticized, however, because it had assumed these systems were governed by purely deterministic and stationary processes. In addition, Schaffer (1985) pointed out a major limitation of attractor reconstruction: it is near impossible to prove that an attractor is time-invariant. For example, when there are major shifts in the qualitative dynamics of a system, such as in the Canadian lynx data, there is no way of knowing whether this is a stochastic result of latent, complex geometry in the basins of attraction, or a deterministic result of non-stationary population parameters, which alters attractor geometry.

Convinced that stochastic factors had to play some sort of role in governing population fluctuations, ecologists remained skeptical of the importance of deterministic non-periodic chaos - especially the sort of low-dimensional chaos arising from unrealistically nonlinear recruitment (Berryman & Millstein 1989). Theoreticians continued to develop methods for distinguishing between stochastic variability and chaos

(Sugihara & May 1990). Meanwhile, realizing that determinism and stochasticism were not really alternative hypotheses (Hastings *et. al.* 1993), empirically minded theorists were developing new analytical techniques for the detection of chaos in stochastic systems (Ellner 1991, Ellner *et. al.* 1991, 1992, 1995, McCaffrey *et. al.* 1992).

Though interest in chaos in population ecology has waxed and waned over the decades, never was the hypothesis totally dismissed (Turchin & Taylor 1992, Logan & Allen 1992, Hastings *et. al.* 1993). Indeed, a consensus began emerging from these reviews: chaos might be important in those ecological systems where
(1) populations were regulated by highly nonlinear feedback;
(2) density-dependent survival was lagged over time;
(3) population fluctuations were forced by environmental periodicity such as seasonality;
(4) populations were inextricably linked to the collective dynamics of community-level food webs characterized by hyper-connectivity, or high dimensionality.
A second point of agreement was that detecting chaos might be extremely challenging given unreasonably demanding data requirements (*e.g.* thousands of observations (Sugihara & May 1990)) and unreasonably rigid assumptions that could not be met with real ecological time-series data.

More recently, Ellner & Turchin (1995) presented a method for detecting chaos in stochastic systems that is more modest in its demands and assumptions. In applying their technique to 72 data sets, they reach the conclusion that many systems seem to lie at the border between stability and chaos, but relatively few cross over into the chaotic domain. They suggest that the concept of global stability, while useful for some systems (*e.g.* Dennis *et. al.* 1995), must give way to the concept of local stability because many systems that are generally stable often plunge into brief episodes of chaos, and then return to near-stability. Accordingly, they suggest that the distribution of local Lyapunov exponents, and their pattern in time and phase-space, are a more informative indicator of a system's behaviour than a single, global Lyapunov exponent. Their results have received much attention, in part because of the conservativism of their methods and the robustness of their comparative theoretical and empirical approach.

5.1.3 Dynamics of forest tent caterpillar outbreaks

The forest tent caterpillar, *Malacosoma disstria* (Hbn.), exhibits occasional population eruptions that are organized into large-scale outbreaks in the northern part of its range (Hildahl & Reeks 1960, Sippell 1962, Ives 1973, Hodson 1977). Outbreaks in the southern part of its range, from Louisiana to Florida, are much less regular, occurring rarely and sporadically, but in some cases persisting for many years (Batzer & Morris 1978).

Outbreak cycles are most highly synchronized in Ontario, where they recur at thirteen year intervals (Sippell 1962, Daniel & Myers 1995). In the northcentral United States, the periodicity of outbreaks lies between six and sixteen years, with a mean of about ten years (Witter 1979). Outbreaks in the provinces of Saskatchewan and Manitoba (which lie between Alberta, to the west, and Ontario, to the east) have been described as being only weakly periodic, recurring at six-to-sixteen year intervals (Hildahl & Reeks 1960). Dendroecological reconstructions of forest tent caterpillar outbreaks in Alberta suggest that population fluctuations are neither periodic nor random, but lie somewhere in between (Fig. 3.2), with a variable period between six and sixteen years (Fig. 3.8) that is embedded in a broad spectrum of pink noise (*sensu* Halley 1996 and Heino 1998). Thus there appears to be some geographic variation in outbreak frequency and synchrony.

There are three reasons to suspect that forest tent caterpillar population dynamics may be chaotic. First, forest tent caterpillars are prodigious reproducers (Witter & Kulman 1969), yet spectacular outbreaks often collapse suddenly as a result of density-dependent parasitism (Sippell 1962) and disease (Stairs 1966, 1972). In theory, species with these life history traits are more likely to exhibit chaotic dynamics (May 1974). Second, the magnitude of outbreaks seems to vary somewhat discretely in Alberta. For example, alternating pulses of severe and mild outbreaks are especially obvious at Dixonville, Peerless L., Athabasca, Drayton Valley, and Cooking L. (Fig. 3.2). Such behaviour can signify periodic environmental forcing associated with quasi-periodic and chaotic strange attractors (Schaffer 1985, Logan & Allen 1992). Third, peaks in the power spectra of tent caterpillar abundance are broad and flat (Fig. 3.8), just as one would expect for chaotic time-series (Casdagli 1991).

5.1.4 Objective of this study

The goal this chapter is to analyze the stability of temporal fluctuations in regional outbreaks of forest tent caterpillar in Alberta. By distinguishing between global (*i.e.* long-term) and local (*i.e.* short-term) stability the question is not merely whether tent caterpillar outbreaks are chaotic, but whether there is some pattern to the emergence of temporary instances of unstable behaviour. Are there, for example, specific junctures where populations become de-stabilized? It would be particularly informative if episodes of local chaos coincided with the triggering of some well-known environmental or biotic event. By examining the stability properties of outbreaks in nine municipalities across Alberta, it is hoped that some common patterns will emerge that could help to explain the seemingly erratic behaviour of forest tent caterpillar populations found in all parts of the province and across the Canadian prairies.

5.2 Methods

5.2.1 Outbreak disturbances revealed in aspen ring width chronologies

Chapter three presented detrended trembling aspen (*Populus tremuloides* Michx.) ring width chronologies for 246 stands located in nine municipalities across northcentral Alberta. Stands were aggregated in the form of a 3x3 grid covering 93 500 km^2, and 128 of these stands were evenly distributed over a 420 km^2 area immediately southeast of Cooking Lake, which is located near Edmonton, on the southcentral part of the provincial grid (Fig. 2.1).

Fluctuations in aspen ring widths in western Canada are highly indicative of the effects of defoliation during large-scale outbreaks of forest tent caterpillar (Hogg 1999). Corroborating this view are: (1) results in chapter three indicating that decadal fluctuations in spring precipitation were limiting aspen growth only in the aspen parkland and (2) results in chapter six showing that there is a substantial portion of fine-scaled joint spatiotemporal variability that can not be attributed to a macro-scale process such as decadal cycles in spring precipitation, but may be attributable to quasi-synchronous tent caterpillar outbreak.

5.2.2 Data analysis

All analyses were conducted using S-plus (MathSoft Inc.). Nonlinear stability analysis was performed using the FUNFITS package (Nychka *et. al.* 2001), which provides functions for neural net regression and estimation of Lyapunov exponents, among others. The algorithm for estimation of Lyapunov exponents is equivalent to that of LENNS (S. Ellner, personal communication), which is specially designed for stability analysis in noisy nonlinear systems (Ellner *et. al.* 1992) and has been used successfully in the analysis of stability in animal population fluctuations (Ellner & Turchin 1995).

5.2.2.1 Autocorrelation analysis

Turchin & Taylor (1992) showed that the autocorrelation structure in population time-series data could be used to diagnose stationarity and endogenous periodicity in fluctuations. Two key parameters of the autocorrelation function (ACF) are the pattern of damping, which could be either oscillatory or exponential, and the rate of damping. To determine whether forest tent caterpillar outbreaks were stationary and periodic, ACF's were computed for aspen ring width data from each of nine municipalities in Alberta. To determine whether periodic fluctuations might be a product of a "phase-forgetting" process, partial autocorrelation functions (PACF) were also estimated. The presence of high-order partial autocorrelations would suggest a "phase-remembering" cycle resulting from periodic environmental forcing. A prelude to nonlinear stability analysis, these analyses would provide a preliminary indication whether forest tent caterpillar outbreaks might be governed by complex dynamics.

5.2.2.2 Stability analysis

Adopting the approach outlined by Ellner & Turchin (1995), nonlinear stability analysis was used to investigate whether forest tent caterpillar outbreaks in Alberta recur chaotically. Briefly, nonlinear stability analysis involves a two-stage process whereby data are modeled using a nonlinear autoregressive technique and then Lyapunov exponents are estimated from the model. Note the goal of nonlinear time-series modeling is not data interpretation, but data description for the purpose of stability analysis.

5.2.2.2.1 Neural net regression

Municipal aspen ring width chronologies spanning 1908-1994 were modeled using artificial neural net regression. This is a non-linear autoregressive technique that uses feed-forward artificial neural networks to describe the relationship between a continuous state variable at a given time and system states at previous times (Ellner & Turchin 1995). A single hidden-layer model with a variable size of one to four hidden units ($k = 1$ to 4) was parameterized using a third-order time-lag (embedding dimension $d = 3$). With an embedding dimension of three, the use of four units implies $1 + k\,(d + 2) = 21$ model parameters (Nychka *et. al.* 2001), yielding an over-parameterized model that is highly likely to fit the data, but at an increased risk of falsely detecting chaos (Ellner & Turchin 1995).

Feed-forward neural net (FNN) regression has been compared to some other nonlinear modeling techniques and has proven to be as powerful a modeling tool as response-surface methodology (RSM) and estimation with thin-plate splines (TPS) (Ellner & Turchin 1995). In particular, unlike other nonlinear techniques, FNN is especially useful for nonlinear stability analysis because it is robust against errors in choosing the correct embedding dimension (McCaffrey *et. al.* 1992). Applied in the context of population modeling, parameters estimated by FNN regression are not meant to be interpreted in the same meaningful way that they can in true network modeling (Ellner & Turchin 1995). The value of the technique lies in its empirical power in simulating nonlinear dynamic processes with a minimum of assumptions.

Typically, models are optimized for nonlinear stability analysis by choosing the degree of complexity that minimizes a quantity known as the generalized cross-validation

(GCV) (Nychka *et. al.* 2001). Without knowing the structure of the generating process (*e.g.* how much of the dynamics are due to nonlinearity and how much to stochasticity), it is difficult to judge whether a particular GCV function is appropriate, and it is therefore difficult to decide what level of model complexity (determined by the number of hidden units, in the case of FNN) provides the best approximation for stability analysis (Ellner & Turchin 1995). Consequently, for the present study, stability was analyzed both for those models with minimal GCV and also those that provided the best fit to the data (measured by the coefficient of determination). The first condition leads to a lower chance of detecting chaos while the second leads to a higher chance of detecting chaos (Ellner & Turchin 1995). An unambiguous inference is possible if and only if both models exhibit the same degree of stability.

5.2.2.2.2 Estimation of global and local Lyapunov exponents

In stability analysis, the Lyapunov exponent is an estimate of the exponential rate of divergence away from an attractor given a perturbation of arbitrarily small size. Positive Lyapunov exponents indicate extreme sensitivity to perturbation (chaos) and rapid divergence from a trajectory. Negative values indicate rapid convergence toward a trajectory, implying stable fluctuations even when the process is randomly perturbed.

A global Lyapunov exponent is an estimate of the mean tendency to diverge from an attractor, measured over the entire attractor domain. A local Lyapunov exponent estimates the same tendency to diverge, but it is measured over a part of the attractor domain (*i.e.* for a given time-horizon). A long time-series can be divided into many such horizons and the local Lyapunov exponent can be estimated for each. Confidence limits can be constructed and individual estimates of local Lyapunov exponents can be plotted in time or phase-space to examine heterogeneity in the attractor's stability properties.

Global Lyapunov exponents were estimated from neural net regression models of each municipal aspen ring width chronology. Estimation was based on first-order Taylor expansion. Using the method of Bailey *et. al.* (1998), the distribution of local Lyapunov exponents was also examined because chaos might not be equally pervasive through time.

Briefly, this technique involves estimating local Lyapunov exponents over successively smaller time horizons in order to detect whether there are portions of state-space (*i.e.* moments in time) where a trajectory is extremely sensitive to perturbation. This allowed for the possibility that outbreaks might be globally stable, with some localized instability.

5.3 Results

5.3.1 Autocorrelation structure

The autocorrelation functions of aspen ring widths from 1908-1994 indicated three modal patterns referred to as "boreal", "parkland" and "eastern", according to the location where that mode was dominant (Fig. 5.1). The boreal mode, represented by Dixonville, Peerless L., Fort McMurray, and Athabasca, was characterized by a 15-year cycle, which was statistically significant only at Peerless L., although the half-cycle was significant at all four municipalities. The parkland mode, represented by Whitecourt, Drayton Valley, and Cooking L., was characterized by a 10-year cycle, which was statistically significant only at Whitecourt and Drayton Valley. The half-cycle was significant in all three municipalities. The eastern mode, represented by Conklin and Frog L., was characterized by no apparent cyclicity. Here, none of the negative lags were significant, suggesting no sign of even a half-cycle.

In cases where 15-year and 10-year cycles were not statistically significant, this was a result of weak periodicity at multiple frequencies rather than a distinct lack of periodicity. For example, autocorrelation functions for Dixonville and Cooking L. indicated some bi-modality over lags 13 to 20 and lags 7 to 12, respectively (Fig. 5.1).

Partial autocorrelation functions for all municipalities indicated positive first order feedback and negative second-order feedback, which is characteristic of an endogenously-driven, phase-forgetting cycle (Turchin & Taylor 1992). None of the PACF's truncated after the second lag, however, indicating outbreak dynamics were not well described by a linear second-order autoregressive model (Royama 1992). Defoliating outbreaks are therefore governed either by nonlinear feedback or high-order forcing by some recurring environmental perturbation (Turchin & Taylor 1992). On the other hand, given that a slowly damping PACF should be expected from a moving average process (Royama 1992), negative partial autocorrelations for high-order lags may not be indicative of outbreak dynamics if aspen growth is a moving average process.

These results suggest that forest tent caterpillar outbreaks in Alberta are a stationary and near-periodic process. Of course, stationarity in outbreak dynamics may be exaggerated by the fact that individual stem-level aspen ring width chronologies were filtered to remove stem- and stand-level growth trends. For example, detrending could have inadvertently removed low-frequency variability attributable to non-stationary aspects of tent caterpillar outbreak dynamics.

5.3.2 Stability analysis

5.3.2.1 Neural net regression

In all municipalities, the single-unit neural net regression model, which employed six parameters, produced the minimum generalized cross-validation (GCV). The single-unit models accounted for an average of 30% of the variation in aspen ring width (Fig. 5.2, first column). Models with two, three, and four hidden units (11, 16, and 21 parameters) provided a better fit to the data but had successively higher GCV's. Models with four hidden units accounted for an average of 60% of the variation in aspen ring width (Fig. 5.2, second column), but exhibited large GCV values.

The large difference in model performance with one *versus* four units was due mainly to differences surrounding low-frequency, high-amplitude disturbance pulses affecting aspen growth, and not to differences surrounding high-frequency, low-amplitude noise (Fig. 5.2, first *vs.* second columns). If residuals from the single-unit model were due mainly to non-outbreak related variability in aspen growth (*e.g.* growth-inhibition caused by drought and growth-promotion caused by nutrient pulses) then the single-unit model results might provide the best indication of outbreak dynamics. If additional variation explained by the four-unit model could indeed be attributed to tent caterpillar outbreak dynamics then this model would offer a better reconstruction. Given the large GCV of the four-unit models and the potential importance of climatic noise in the aspen ring width chronologies, the single-unit simulations provided the most conservative test for the presence of chaos in tent caterpillar outbreaks.

5.3.2.2 Global and local Lyapunov exponents

Stability analysis of the single- and four-unit neural net regression models yielded different results, but with a consistent geographical pattern. With the single-unit model, none of the municipal aspen ring width chronologies exhibited a positive global Lyapunov exponent (GLE), but there was a notable trend toward larger GLE's (lower stability) at Drayton Valley, Cooking L. and Athabasca (Fig. 5.3, left column). With the over-parameterized four-unit model, those same municipalities exhibited positive GLE's, as did Frog. L and Fort McMurray, indicating chaotic outbreak dynamics (Fig. 5.3, second column). Although outbreak oscillations appeared to be generally non-chaotic, fluctuations on the southwest portion of the provincial grid appeared to be less stable.

The pattern of variation in local Lyapunov exponents (LLE) from the four-unit models was not surprising given the large GLE's: whether estimation was based on short or long time horizons, the 95% confidence interval stretched into the positive range, indicating a weak possibility of local chaos (Fig. 5.3, right column). The pattern of variation in LLE's from the single-unit models was rather interesting: although no confidence interval was wide enough to extend much above zero, the tendency toward higher values was definitely stronger when stability was estimated over smaller time horizons (Fig. 5.3, first column). The trend is particularly obvious at Whitecourt, Drayton Valley, and Cooking L. for LLE's based on time horizons of five years. The tightness of confidence intervals here suggests that while the probability of even local chaos might be low, population fluctuations are only borderline-stable in the short-term. That the LLE's diminish for longer time horizons suggests that borderline local stability gives way to more robust longer-term stability.

The distribution over time of 5-year LLE's indicates an interesting pattern in the emergence of short-term chaos (Fig. 5.4). In the boreal locations, there are four bouts of instability (LLE > 0) associated with the occurrence of major province-wide FTC outbreaks (Fig. 5.4, left column). Episodes of instability begin during the onset of weakly synchronized outbreak pulses around 1918, 1937, 1957, and 1977, and they terminate a few years later with the collapse of those smaller outbreaks and the resurgence of major, synchronized, province-wide outbreaks in 1924, 1942, 1962, 1982. In contrast, outbreak dynamics in the parkland region are borderline-stable and there is no marked change in the stability properties over time (Fig. 5.4, right column). Apparently chaotic behaviour in the early part of the Frog L. aspen ring width chronology is likely a result of poor replication in that municipality.

The good match in the boreal region between the temporal pattern of local destabilization and the occurrence of large-scale outbreaks some years later is clarified when the LLE's and ring widths from the five boreal municipalities are averaged and plotted in time or phase-space (Fig. 5.5). The correlation between 5-year LLE's and aspen ring widths four years later is $r = -0.72$, implying that the amplitude of an outbreak is harder to predict than is the timing of a population cycle.

5.4 Discussion

5.4.1 Inferring outbreak stability from tree ring widths

A fundamental problem with the present study is that aspen ring widths give only a broad indication of the occurrence of past insect outbreaks. Tree ring widths, while being largely determined by herbivore loads, are also subject to their own endogenous and exogenous sources of deterministic and stochastic variability. The magnitude of this variability is unknown and so it is unclear what effect ignoring this source of variation might have on the ability to detect chaos in insect outbreak dynamics.

A second problem is that it is not known precisely how aspen ring widths scale to tent caterpillar densities. Unfortunately, Lyapunov exponents estimated by non-linear stability analysis are sensitive to scaling in the source data (Casdagli 1991). Casdagli

(1991) explained how log-transformation of measles data by Ellner (1991) was the key to refuting the claim of Sugihara & May (1990) that infection cycles were chaotic. [Instead, it appears infection rates are subject to multiplicative noise. Ellner's (1991) insight was this: if a system is truly chaotic, then simple transformation will never decrease the Lyapunov exponents below zero.] Given that the Lyapunov exponents of tent caterpillar outbreak data were usually negative, could this be due to a lack of a suitable scaling transformation of aspen ring widths? This question is of general importance, but it is not addressed in the literature.

These caveats aside, results from previous and future chapters suggest aspen ring widths may be a fairly good indicator of log-scaled tent caterpillar densities.

5.4.2 Irregular temporal dynamics

Autocorrelation analysis showed that the periodicity of forest tent caterpillar outbreaks is roughly 15 and 10 years respectively in the boreal and parkland regions of Alberta. However, because large-scale outbreaks tend to occur at irregular intervals the dynamics are only weakly periodic in several municipalities. Such weak periodicity suggests large-scale outbreaks are not merely the product of a limit cycle induced by a simple host-parasitoid interaction. Phase coherence analysis (Lindström 1997) may be a more effective technique for detecting periodicity in short and noisy time-series data, and this promising technique should be investigated.

If the single-unit neural net regressions adequately represent the chronology of forest tent caterpillar outbreaks, then irregularities in outbreak occurrence are not due to chaos because global and local Lyapunov exponents derived from these simulations were generally negative, indicating stable population fluctuations. But if the four-unit FNN models more faithfully capture the dynamics of FTC outbreaks, then outbreaks may be governed by chaos. At issue is, first, whether the additional variation explained in the four-unit models might instead be attributable to vegetation dynamics independent of outbreak dynamics, and second, failing this, whether the additional explained variation is due to deterministic or stochastic aspects of tent caterpillar dynamics. If the additional variation explained by the four-unit FNN model is indeed deterministic in origin, then chaos is likely. But if, as the single-unit model suggests, it is actually stochastic in origin, then chaos is unlikely.

Two points favour the latter view. First, the GCV of the four-unit model is so high that independent model validations would probably fail to reproduce the same degree of predictive power, implying the four-unit model is over-parameterized. Second, that the PACF's of aspen ring widths do not truncate after two time-lags implies the system may be perturbed by low-frequency, high amplitude noise. This would be in keeping with the view that climatic perturbations, especially winter temperature, may play a vital role in the dynamics of tent caterpillar populations.

If irregular dynamics are not a result of chaos, can they be explained by a stochastic hypothesis? Simple theoretical models suggest the answer is 'yes'. First, as explained by Bulmer (1976) and illustrated by Kaitala *et. al.* (1996) deterministically damping oscillations generated by a linear second-order difference equation can be prevented from damping by stochastic random perturbation. Second, as shown by Barbour (1990), the amplitude of oscillation in a linear model is proportional to the noise variance. Third, as shown by Royama (1984), a favourable sequence of stochastic perturbations can lead to a heightened amplitude of oscillation such that the occurrence of an "outbreak" may simply depend on whether a given population cycle happens to exceed some arbitrary tolerance threshold. Over time, oscillations tend to vary in amplitude in an unpredictable way, even though the periodicity is fixed. Thus if forest tent caterpillar outbreak cycles are a result of deterministically damping population oscillations that are held aloft by stochastic perturbation, then the degree of irregularity caused by aperiodic super-decadal outbreaks could be a result of stochastic amplitude modulation.

The issue is important in part because populations that are governed by chaos are resistant to the synchronizing effect of dispersal and correlated perturbation (Allen *et. al.* 1993). If forest tent caterpillar populations are indeed fundamentally oscillatory and non-chaotic, then poor synchrony of outbreaks is not a result of ill-behaved local population dynamics, but is due to a lack of connectivity, either by dispersal (Barbour 1990) or correlated perturbation (Moran 1953), among local populations.

5.4.3 Spatial gradient in stability

In the same way that the autocorrelation analysis suggested a distinction between boreal and parkland outbreak periodicity, stability analysis suggested a distinction between boreal and parkland outbreak stability. Although global Lyapunov exponents derived from the single-unit model were negative for all municipalities, they were significantly higher in Whitecourt, Drayton Valley and Cooking L. These were the same municipalities where (1) local Lyapunov exponents were higher than global Lyapunov exponents and (2) local Lyapunov exponents did not vary much over time. Clearly there is something different about the southwest. Interestingly, provincial aerial defoliation surveys in 2000 and 2001 have indicated Drayton Valley populations have already reached outbreak status, while the remainder of the province has not. This suggests Drayton Valley may again be poorly synchronized with the remainder of the province over the course of the next large-scale outbreak.

Across municipalities, the degree of stability in outbreak dynamics was positively related to the performance of the single-unit FNN regression model (Fig. 5.6). In fact, the municipalities clustered into two distinct groups (Fig. 5.6, top). High stochasticity and high stability was observed in the northeast/boreal, while low stochasticity and low stability was observed in the southwest/parkland (Fig. 5.6, bottom). Thus it appears that FTC populations may be regulated in different ways in different parts of the province.

Ellner & Turchin (1995), in a similar study of many animal species, remarked how, in general, R^2 tends to be positively correlated with the Lyapunov number ($\gamma = \exp(GLE)$). They suggested that high stability and stochasticity is a result of equilibrium dynamics being dominated by density-independent perturbation, while low stability and stochasticity is a result of low-frequency periodicity induced by lagged density-dependence outweighing density-independent perturbation effects. According to this interpretation, it would appear that FTC dynamics in northeastern Alberta may be dominated by density-independent fluctuations caused by climate or dispersal, while dynamics in southwestern Alberta may be dominated by periodic fluctuations induced by lagged density-dependence. Comparing FTC stochasticity and stability to values calculated by Ellner & Turchin (1995) for field populations of various animal species, northeast FTC populations ($R^2 \approx 0.21$, $\gamma \approx 0.42$) fluctuate much like Norfolk hare ($R^2 = 0.20$, $\gamma = 0.34$), while southwest FTC ($R^2 \approx 0.38$, $\gamma \approx 0.68$) fluctuate much like Aberdeenshire red grouse ($R^2 = 0.35$, $\gamma = 0.58$) and Norfolk partridge ($R^2 = 0.39$, $\gamma = 0.59$).

If FNN regression models perform differently with data sets exhibiting different kinds of dynamics, then it is possible that geographic patterns in apparent stochasticity and stability of FTC outbreaks could be an artifact of the modeling technique used in simulating the source data. For example, it is possible that the influence of stochastic effects, such as periodic environmental forcing and periodic noise, may lead to false inferences of chaos if such effects are not explicitly removed in the modeling stage. In the case of FTC in Alberta, if dynamics in the southwest are driven by stochastic periodicity, then populations may be mis-diagnosed as unstable if they are modeled within a purely deterministic framework. It would therefore be instructive to examine the robustness of Ellner & Turchin's (1995) method when applied to complex time-series generated by simulation models with known stability properties.

5.4.4 Modeling chaos

5.4.4.1 Mechanism underlying temporary destabilization of FTC

The biological mechanism behind temporary instability in FTC dynamics is unknown, but two possibilities are envisioned. First, if epidemic populations increase gradually in their vulnerability to perturbative collapse, then the termination of a population cycle may be highly unpredictable, depending on the precise timing and intensity of an appropriate perturbation. If, for example, winter and spring temperatures involve significant nonlinear (*i.e.* partially density-dependent) perturbation effects (chapter eight), then regional differences in winter and spring climates could induce short-term population instability. The variable length of the time taken for a population to collapse could explain why outbreak amplitude varies temporally. Second, the rate of increase of endemic populations may depend sensitively on the precise composition of the community of relevant predators and parasitoids. Parasitoid community structure, in turn, may depend sensitively on the outcomes of competitive interactions at low host densities, and therefore may vary from one population cycle to the next. Notably, neither of these mechanisms involves severe nonlinear feedback, but both may account for apparently chaotic host population dynamics.

5.4.4.2 Low-dimensional chaos in high-dimensional systems

Populations regulated through high-dimensional community-level interactions (*e.g.* among predators, parasitoids, hyper-parasitoids, alternate hosts, and alternative prey) may fluctuate in a manner that resembles low-dimensional chaos, and, indeed, they may be modeled as low-dimensional chaotic processes (Casdagli 1991). However, doing so ignores the important processes at play. If the goal of stability analysis is simply to summarize the predictability of a system, this is not a problem. But if the goal is to understand the origins of complex dynamics, there is a danger of over-interpretation. Complex dynamics are not necessarily indicative of nonlinear dynamics.

5.4.4.3 Static *versus* dynamic attractors

Presumably, the goal of reconstructing an attractor is to make a statement about a system's long-term, asymptotic behaviour. But what if its long-term behaviour does not reflect its asymptotic behaviour? What if its asymptotic behaviour changes over time, as a result of gradual changes in its deterministic, density-dependent structure?

In the case of tent caterpillars, long-term changes in forest structure and climate could influence higher-order biotic interactions, thereby causing non-stationarity in dynamics that would be difficult to detect statistically. Similarly, low-frequency fluctuations in climatic parameters could affect the structure and function of community-level interactions. Such structural changes would result in complex non-asymptotic behaviour. Therefore a reconstructed attractor might reflect the long-term dynamics, but not the asymptotic dynamics. In such a case, it makes sense to ask whether observed complexity is due to asymptotic dynamics, or non-stationarity. Understanding a system's dynamics may therefore require a dual approach to attractor reconstruction and interpretation.

If attractors are time-dependent structures, this would seriously limit the potential success of current attractor reconstruction methodologies. For it may be that attractors are sufficiently dynamic that they can not be reconstructed even with continual observation. Is attractor reconstruction like shooting at a moving target? How much change do attractors go through? How does their geometry vary, and over what sort of time-scales? Are they elastic or plastic?

The notion that attractors may be time-varying cuts at the very heart of the chaos debate. It has been asked whether mother nature is a strange attractor (Hastings *et. al.* 1993). It may be that the attractors that govern nature only appear to be strange when viewed from an unnaturally static perspective.

There has been, over the last four decades, a similar debate regarding the relative merit of static double-equilibrium models (*e.g.* Southwood & Comins 1976, Ludwig *et. al.* 1978, Gould *et. al.* 1990, Campbell 1993, Elkinton *et. al.* 1996) *versus* dynamic equilibrium models (Royama 1984, 1992) in describing the behaviour of insect outbreaks. This particular battle seems to be nearing the point of stalemate as researchers begin to recognize these views are not as incompatible as once thought.

In both cases what is required is a synthesis that accounts for the similarities and differences between these divergent viewpoints. A useful synthesis would demonstrate: (1) how the static attractor paradigm emerges naturally as an abstract description of the behaviour of more complex process models of real systems, and (2) how the behaviour of realistic process-oriented models and their abstractions may be shown to differ under specific experimental regimes. This would help clarify the mutualistic roles that theoretical and empirical investigations can play in elucidating the dynamics of actual ecological systems. Identifying opportunities for relating ecological theory to data is a key to progress in the understanding of ecological dynamics.

5.5 Conclusion

Forest tent caterpillar outbreaks in Alberta appear to be somewhat periodic, but the degree of regularity and the period of oscillation varies geographically. The stability and predictability of outbreaks also varies in a systematic, geographic manner. The gradient of stable, stochastic dynamics in the northeast to less-stable, deterministic dynamics in the southeast appears to be robust and therefore demands an explanation. One possibility worth testing is that southwestern populations may be more vulnerable to sub-decadal periodic environmental forcing.

The complex dynamics of forest tent caterpillar outbreaks in Alberta appear not to be a product of chaos. This conclusion could also be bolstered by: (1) nonlinear modeling with other techniques, such as RSM and TPS; (2) validating these models with comparable datasets from additional sampling points; (3) analysing the stability of longer outbreak time-series; and (4) analysing the stability properties of realistic process-models. Natural survivorship studies and manipulative experimentation will be crucial for structuring and parametrizing such process models.

Our collective inability to explain and predict the occurrence of quasi-synchronous outbreaks may be more a function of our limited understanding of the system's stochastic behaviour than any limitations imposed by chaos. This conclusion assumes that the highly stable single-unit neural net regression models are indeed more appropriate than the better-fitting four-unit models that indicate chaotic behaviour. A deeper analysis into the behaviour of GCV under different stochastic process-models with known dynamics would provide greater assurance that it is a judicious discriminant.

If ecological attractors in the real world are time-varying, then the static-attractor paradigm is inappropriate and analytical methods that assume as much will be in error. It is unknown how sensitive modern stability analyses are to complex dynamics induced by interactions between non-stationary stochastic and deterministic processes, but this should be examined by conducting nonlinear stability analysis on a variety of general, but suitably complex simulation models.

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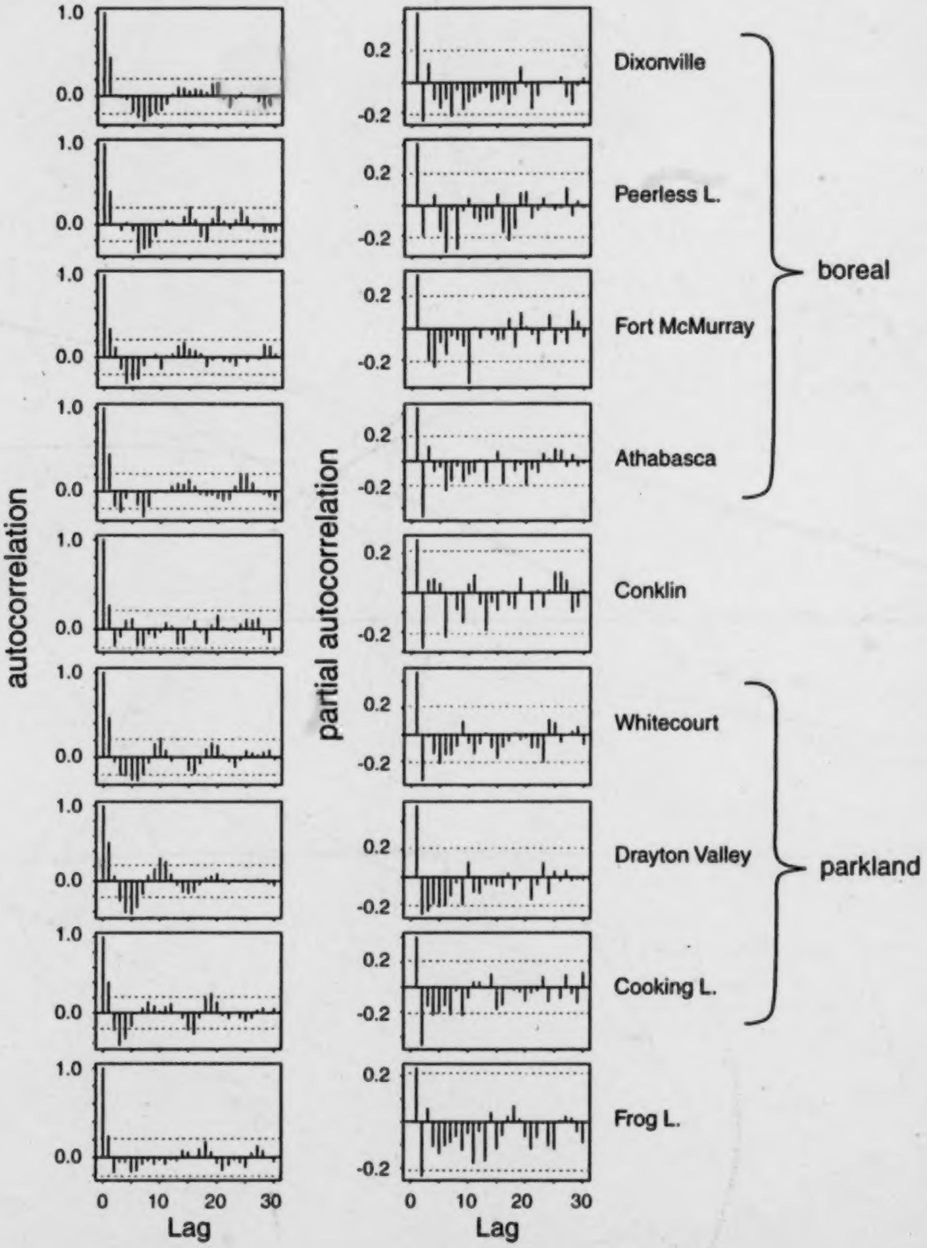

Figure 5.1. Autocorrelation and partial autocorrelation functions for municipal aspen ring widths 1908-1994. Dashed lines indicate 95% confidence intervals (Bartlett bands).

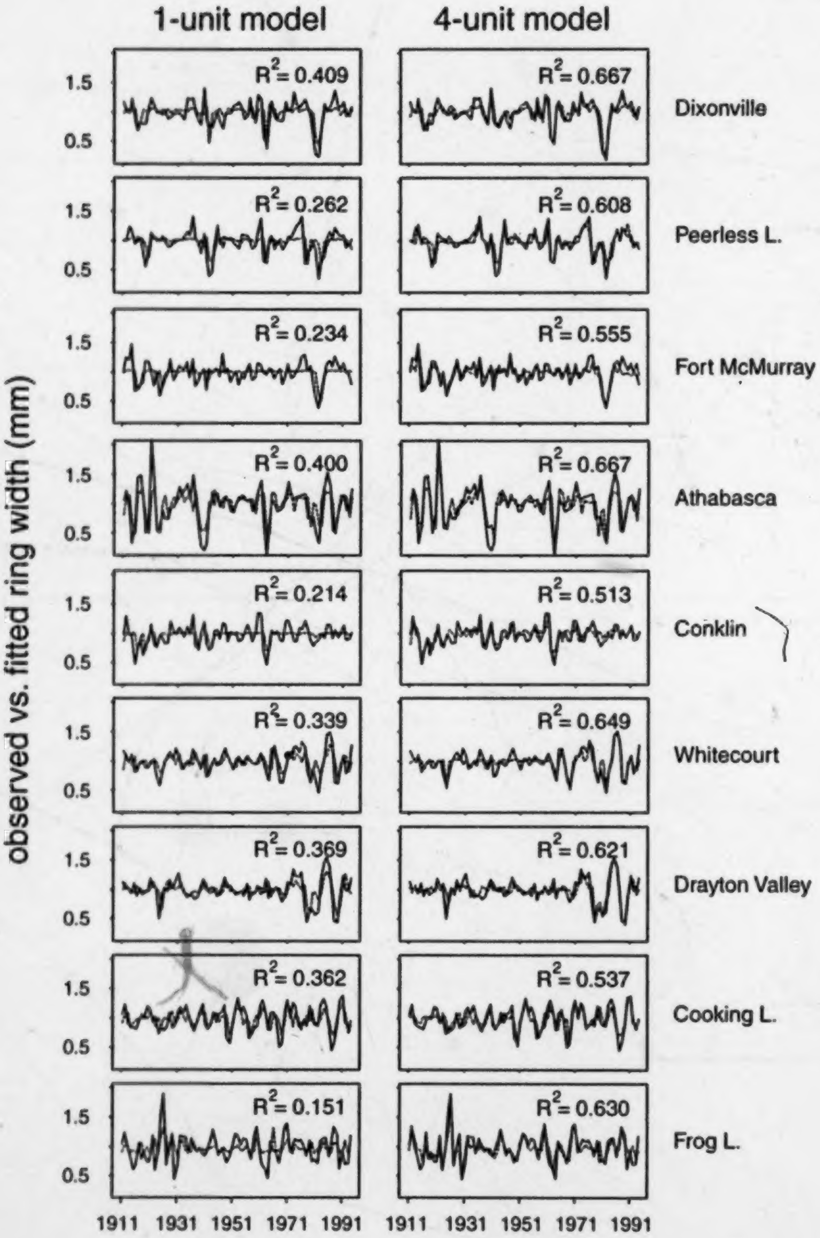

Figure 5.2. Results from neural net regression. Fitted values shown as dotted line.

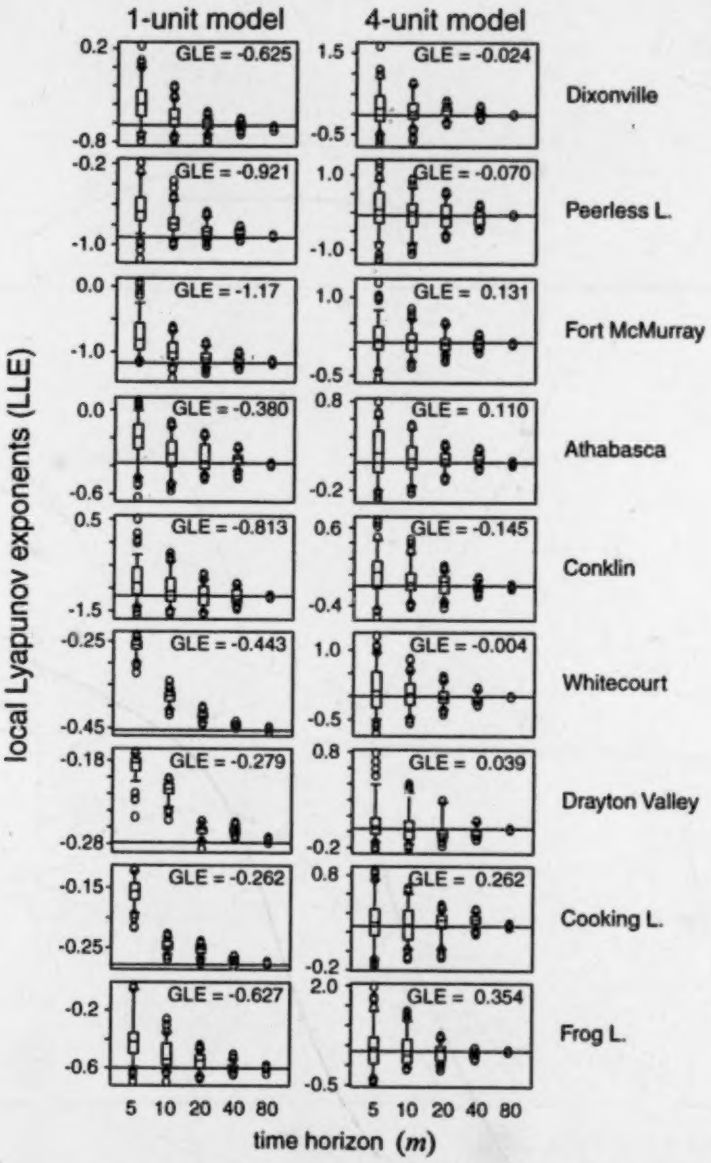

Figure 5.3. Non-linear stability analysis of municipal aspen ring width chronologies (GLE = global Lyapunov exponent). Lower Lyapunov exponents imply higher stability. LLE's for *m* = 5 from single-unit model plotted against time in Fig. 5.4.

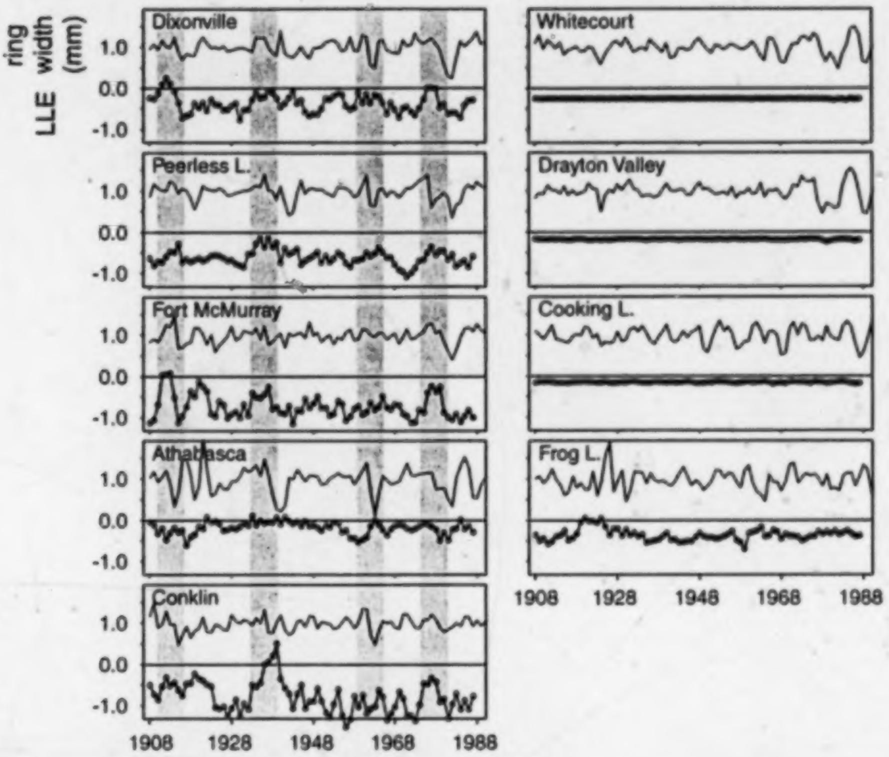

Figure 5.4. Local Lyapunov exponents (circles) estimated from 1-unit neural net regression model, for 5-year time horizon (see Fig. 5.3), plotted over time along with detrended aspen ring width (lines). Left column indicates boreal municipalities with super-decadal episodes (bars) of short-term chaos (LLE > 0) and borderline instability (LLE ≈ 0). Right column indicates parkland municipalities with persistently borderline-stable outbreak dynamics that never turn chaotic. The four major bouts of instability in the boreal region are associated with complex patterns of FTC outbreak development where small outbreaks in 1918, 1937, 1957, and 1977 precede larger-scale super-decadal outbreaks in 1924, 1942, 1962, and 1982.

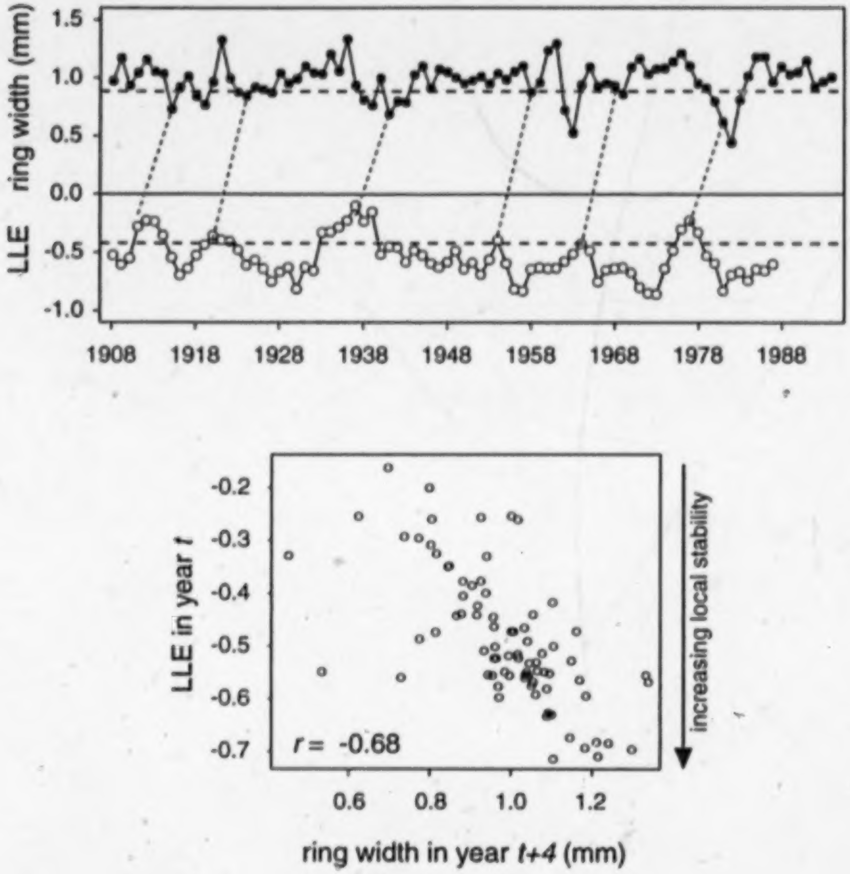

Figure 5.5. Local Lyapunov exponents (LLE) and aspen ring widths from Fig. 5.4, averaged over five boreal municipalities, showing negative association between stability and outbreak impact. Top: six instances where LLE's increased above -0.4, each of which preceded severe outbreaks four years later where aspen ring widths dropped below 0.9 mm. Bottom: significant negative correlation between local Lyapunov exponents and aspen ring width four years later.

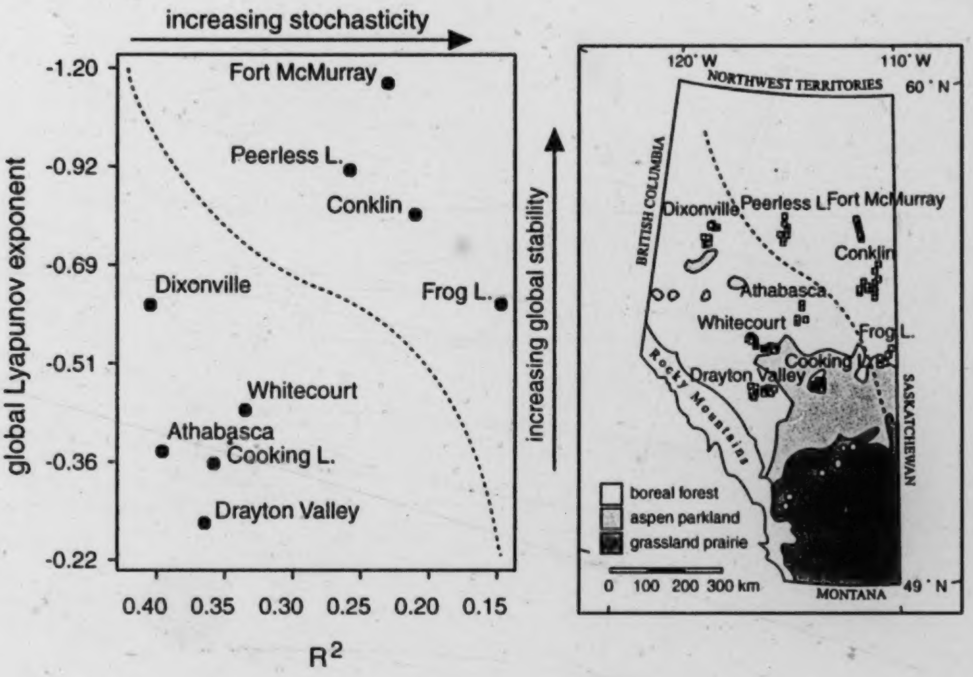

Figure 5.6. Geographic patterns in stochasticity and stability of FTC outbreak dynamics. Left: Regression R^2 values (from single-unit model in Fig. 5.2) plotted against global Lyapunov exponents (from Fig. 5.3) indicate positive relationship. Highly stochastic and stable dynamics are prevalent in the northeast. Less stochastic and less stable dynamics are prevalent in the southwest. Right: locations of municipalities and individual stands.

6. WHERE, WHEN, AND WHY ARE FOREST TENT CATERPILLAR POPULATIONS IMPERFECTLY SYNCHRONIZED: MULTI-SCALE SPATIOTEMPORAL ANALYSIS OF OUTBREAKS IN ALBERTA

6.1 Introduction

6.1.1 Population cycles and synchrony

Much has been made recently of the idea of animal population cycles being synchronized by population teleconnectivity (Ranta *et. al.* 1997, 1998a,b, Myers 1998, Kendall *et. al.* 1999, 2000). According to classical population theory, there are three mechanisms by which population cycles might be synchronized by teleconnective processes: (1) phase-locking by correlated perturbation (Moran 1953); (2) period-forcing by correlated catastrophic disturbance (Berryman 1981); (3) frequency-locking *via* dynamic parametric homogenization resulting from intermigration among sub-populations (Barbour 1990). In practice, however, examples of well-synchronized animal population cycles are uncommon, and the mechanisms underlying synchrony in those rare cases are poorly understood (Hanski & Woiwod 1993).

In fact, even the most exemplary systems, such as spruce budworm and Canadian lynx (Royama 1992), do not exhibit perfect population synchrony across the entire species' range (Candau *et. al.* 1998, Ranta *et. al.* 1997). Other imperfectly synchronized oscillating systems include western tent caterpillar (Myers 2000), Douglas-fir tussock moth (Mason & Wickman 1988, Berryman *et. al.* 1990), European spruce budmoth (Baltensweiler & Fischlin 1988), pine looper (Barbour 1990), and Fennoscandian voles (Ellner & Turchin 1995) and grouse (Ranta *et. al.* 1998a,b).

While much effort has been spent investigating the causes of population synchrony, it would appear that an equally valid question is: why do cyclic populations, in some instances, fail to synchronize perfectly? Is it due to a lack of climatic and population teleconnectivity? Or are local population dynamics not sufficiently well-behaved for these mechanisms to operate? Localized instances of synchrony-breakdown within well-behaved and otherwise synchronous model systems might be informative as to the ecological mechanisms responsible for population cyclicity and synchrony.

6.1.2 Meso-scale synchrony breakdown

6.1.2.1 Demographic stochasticity from dispersal and environmental variability

Barbour (1990), for example, used a simple theoretical model to illustrate how pine looper population cycles in Scotland might be resilient to the synchronizing effect of dispersal as a result of deterministic predator-prey oscillations damping too rapidly for independent populations to have much influence on one another (*e.g.* Ranta *et. al.* 1998a). It was supposed that the appearance of robust population cycles was exaggerated through the amplifying effect of stochastic perturbation, an effect first described by Bulmer (1976) and later by Kaitala *et. al.* (1996). Here, an increase in the tendency toward less damped deterministic oscillations should allow low rates of dispersal to synchronize pine looper population cycles.

Similarly, Berryman *et. al.* (1990) demonstrated how asynchrony in Douglas-fir tussock moth population cycles in the western United States might be a result of the relatively small scale over which perturbations are correlated. Here it was supposed that populations deterministically tended toward slowly damping oscillations, such that the appearance of population cycles was not merely the result of exaggeration by stochastic amplification. Under this scenario, an increase in the degree of spatial correlation in perturbations should lead to increased synchrony - an effect first noted by Moran (1953) and later explored by Royama (1992) and Ranta *et. al.* (1998a,b).

These examples show how studies of meso-scale synchrony breakdown can be informative as to the ecological mechanisms responsible for population cyclicity and synchrony. Yet, in both modeling studies, the assumption that the deterministic dynamics are governed by a well-behaved, single-point attractor was crucial to the analysis.

6.1.2.2 Complex dynamics in spatiotemporal systems

Theoretical investigations have shown that systems governed by highly non-linear processes (May 1976), including dispersal-driven eruptive manifolds (Murray 1993) and strange attractors (Schaffer & Kot 1985) are less easily synchronized by population teleconnectivity (Allen *et. al.* 1993, Solé & Bascompte 1998), suggesting assumptions about a system's deterministic dynamics should be checked before such bold conclusions can be widely accepted. Unfortunately, eruptivity and chaos are not easy to diagnose from time-series of population data alone. Typically, much more detailed demographic information is required, from both natural studies and manipulative experiments, in order to build and then analyze a process-oriented model.

In addition, the self-organization hypothesis of meso-scale synchrony breakdown suggests large-scale spatiotemporal patterning in multi-trophic systems may have little to do with spatiotemporal environmental variability and low-dimensional complexity (Hassell *et. al.* 1992, 1994, Kaneko 1998, Bascompte & Solé 1998). Comprehensive and compelling, this emerging hypothesis is based on theoretical results showing that temporal models, when extended spatially into two-dimensional space, have such a large number of spatial degrees of freedom that: (1) initial conditions and history have a dominating influence on pattern formation (Solé & Bascompte 1998); (2) equilibria are approached so much more slowly than in purely temporal formulations that a long time is spent in a transient state of non-equilibrium (Hastings 1998); (3) spatial and temporal lags associated with local foraging and dispersal play such heightened role in pattern formation that the relative importance of local density-dependent processes diminishes (Wilson *et. al.* 1998). In short, this theory calls into question all those classical ecological ideas that hinge on the assumption that a system's observed behaviour is indicative of its asymptotic, or long-term, behaviour (Hastings 1998).

Spatially explicit predator-prey theory, in particular, shows that high-dimensional chaos is likely to emerge for a wide range of parameters (Wilson *et. al.* 1998), thus reviving the debate about the importance of chaos in animal population dynamics (Berryman & Millstein 1989). Indeed, the numerous field and laboratory populations that do not exhibit low-dimensional chaotic fluctuations (Ellner & Turchin 1995) may, in fact, exhibit higher-dimensional spatiotemporal chaos (Kaneko 1998). The broad implication is that common notions about mechanisms of population synchrony and chaos founded on results from small-scale spatiotemporal models may be overly simplistic. Of particular concern is the relevance of small-network models, such as those of Barbour (1990), Berryman *et. al.* (1990), and Royama (1992), where local predator-prey interactions are represented in a strictly spatially implicit manner.

To assess the relevance of spatially explicit and spatially implicit predator-prey theory to field ecology, it is necessary: (1) to monitor real populations over large spatial scales and at high resolution; (2) to formulate population process models as coupled map lattices, with explicit local dynamics and dispersal rules; (3) to validate major assumptions; (4) to compare predicted and observed spatiotemporal patterns. This is a tall order for any system, but the forest tent caterpillar is a species that seems appropriate because its biology is well-known, there is a long history of modeling its dynamics, and there is now abundant high-resolution spatiotemporal outbreak data available for analysis.

6.1.3 Forest tent caterpillar dynamics at multiple scales

The forest tent caterpillar, *Malacosoma disstria* (Hbn.), exhibits occasional population eruptions that are organized into large-scale outbreaks in the northern part of its range (Hildahl & Reeks 1960, Sippell 1962, Ives 1973, Hodson 1977). Outbreaks in the southern part of its range, from Louisiana to Florida, are much less regular, occurring rarely and sporadically, but in some cases persisting for many years (Batzer & Morris 1978).

6.1.3.1 Outbreak synchrony

Outbreak cycles are most highly synchronized in Ontario, in central Canada (*e.g.* Sippell 1962). But even there they are not perfectly synchronous. In northeastern Ontario, along the Quebec border, outbreaks sometimes lag several years behind the principal 13-year oscillation (Daniel & Myers 1995). Outbreaks in eastern Canada are known to occur, but they have not been documented as carefully or reviewed as comprehensively as in other regions. In the northcentral United States, south of Ontario, the periodicity of outbreaks lies between six and 16 years, with a mean of about ten years, and they are less well-synchronized than in Ontario (Witter 1979). As localized outbreaks can persist anywhere from two to eight years (Hodson 1977), this implies that, at some sufficiently large spatial scale, subsidence of one outbreak in one area tends to overlap with initiation of a different outbreak in another area.

In Alberta, dendroecological reconstructions using trembling aspen have shown that outbreak disturbances there have also had a periodicity between six and 16 years and have varied in spatial pattern and extent (chapter three). Outbreak periodicity is not adequately described by a single parameter, however, because spectral peaks in aspen ring width chronologies occur at both 5-6 years and 10-12 years. Large outbreaks are often followed by a sequence of smaller disturbances.

Outbreaks in the provinces of Saskatchewan and Manitoba (which lie between Alberta, to the west, and Ontario, to the east) have also been described as having a periodicity between six and 16 years (Hildahl & Reeks 1960). Therefore it seems outbreaks may recur less regularly in western Canada. Hildahl & Reeks (1960), however, did not place much value in their estimate of outbreak periodicity. Indeed, the lack of large-scale synchrony in forest tent caterpillar outbreaks across the Canadian prairies caused them to reject the notion of outbreak cyclicity:

> "The periodicity of outbreaks of the forest tent caterpillar has been recognized by Baird (1917) and other authors, but it is questionable as to how periodicity should be measured. Sippell (1957) expressed periodicity as the period between the first years of outbreak, regardless of whether or not the outbreaks were common to specific locations. This method of determining periodicity is satisfactory when individual outbreaks are clearly recognizable, but is not satisfactory under prairie conditions where outbreaks tend to overlap. For this reason it is perhaps advisable to consider periodicity as the time lapse from the first severe infestation at a location to the first infestation of the next outbreak at the same location.

> Application of this procedure to the records of ten selected locations suggests that periodicity may range from six to 16 years with an average of about 10 years. However these figures do not take into account the fact that four of the locations fell within the paths of outbreaks only once during the 35-year period. There is nothing to indicate outbreaks are cyclic."

6.1.3.2 Outbreaks as synchronized population cycles

Clearly, one must be careful not to overstate the case for large-scale synchrony of forest tent caterpillar outbreaks. But it is also important not to overstate the case against the local population cyclicity hypothesis. Here, the distinction between mechanisms of cyclicity and mechanisms of synchrony is crucial. As Royama (1992) has argued: if regional outbreak patterns are determined jointly by local dynamic processes and regional synchronizing forces, then poor regional synchrony of populations cycles may be due to a lack of local population cyclicity or a failure of local cycles to synchronize. Hildahl & Reeks' (1960) rejection of Sippell's (1962) outbreak cyclicity hypothesis therefore does not constitute a refutation of the population cyclicity hypothesis.

Unfortunately, the hypothesis that local populations are inherently cyclic but poorly synchronized is more difficult to test than one might imagine, for a deterministic tendency toward local population cyclicity may not reveal itself in the form of local population cycles. Latent, intrinsic, deterministic local dynamics can be hidden, enhanced or modified by the stochastic, dynamic effects of environmental variability, including migration to and from neighbouring populations. Local population cyclicity might be particularly difficult to ascertain in a large network of interacting populations. This might explain why, even after nearly a century of research, there is no consensus as to the cause of recurrent and regionally synchronized forest tent caterpillar outbreaks.

Currently, the clearest and most convincing hypothesis is that local population cycles are driven by a lagged interaction between caterpillars, parasitoids, and viruses, and these cycles are regionally synchronized by some unknown climatic factor *via* a

Moran effect (Myers 1998). Dispersal also could act as a synchronizing force through Barbour's (1990) mechanism. This, however, depends on the assumption of well-behaved deterministic cycles, which is contentious for two reasons. First, there are several suggestions in the literature that forest tent caterpillar outbreaks may be driven by an eruptive process involving low-density predation or parasitism (Rose 1976, Rose & Harmsen 1981, Roland 1993, Parry *et. al.* 1997), which would imply that dispersal could act as a de-synchronizing force by creating predator-prey diffusive instabilities (Kareiva 1990). Second, although forest tent caterpillar dispersal has not been quantified, parasitoids probably disperse further than forest tent caterpillar larvae and adults, and theoretical investigations into the dynamics of spatial host-parasitoid interactions suggest that high rates of parasitoid dispersal relative to host dispersal favour the emergence of weak, high-dimensional chaotic oscillations (Wilson *et. al.* 1998). This intriguing hypothesis has not yet been formally considered in the forest tent caterpillar literature.

6.1.3.3 Mechanisms of meso-scale synchrony breakdown

Survey studies have shown that outbreaks of forest tent caterpillar last longer in forests that have been fragmented by clearing (Roland 1993, Roland *et. al.* 1998) and that fragmentation in one locality lengthens outbreaks in neighbouring localities (Cooke & Roland 2000). Field experiments have shown that forest clearings and forest edges reduce the effectiveness of parasitoids (Roland & Taylor 1995, Roland *et. al.* 1996) and viruses (Roland & Kaupp 1995, Rothman & Roland 1998) in reducing larval host populations. The most parsimonious explanation is that forest clearing somehow decouples the host-parasite/host-virus interaction - a hypothesis that is supported by spatial patterns of parasitism in heterogeneously forested landscapes (Roland & Taylor 1997, Rothman & Roland 1998). Dynamic decoupling of parasitoids from their hosts has been demonstrated in other systems as well (Kareiva 1990). It is not clear whether it is reduced searching efficiency of natural enemies or the creation of enemy-free refugia that leads to longer tent caterpillar outbreaks. However, either mechanism might be responsible for altering local population dynamics and inducing meso-scale breakdown of synchrony between neighbouring blocks of continuous forest and fragmented forest (Cooke & Roland 2000).

Spatial variation in outbreak amplitude resulting from static spatial landscape effects is only one facet of synchrony breakdown. Little attention has been paid to other aspects of meso-scale synchrony breakdown, such as spatial variation in phasing or periodicity. Studies in other insect systems have addressed the issue of large-scale differences in outbreak phasing (*e.g.* Berryman *et. al.* 1990, Barbour 1990) but these did not address the issue of complex patterns of fine-scaled variation. For example, other studies (*e.g.* Liebhold & Elkinton 1990, Williams & Liebhold 2000) show how, over the course of a large-scale outbreak, local infestations can appear either earlier (focal epicentres) or later in some stands, and they may also collapse sooner or later (refugia). Unfortunately, the temporal dynamics of these systems are unclear, due to limited observations in that dimension.

High-resolution sampling of forest tent caterpillar populations over a 420 km^2 area near Edmonton, Alberta has indicated that, over the period 1993-1996, outbreak populations declined fairly synchronously (chapter two). Little is known, however, about synchrony in the rising phase of outbreak development. If synchronous collapse is caused by correlated perturbation then perhaps the reason fragmented forests experience longer outbreaks is because of reduced build-up of natural enemy populations during the rising phase of a population cycle. This should lead to landscape-related patterns of regionalized outbreak asynchrony, and this is a pattern that can be detected using modern multivariate pattern analysis on historical outbreak data.

6.1.4 Objectives of this study

A closer analysis of spatiotemporal patterns of forest tent caterpillar outbreak disturbances in Alberta might indicate the extent to which synchrony relies on correlated weather patterns and regional connectivity. In particular, spatiotemporal analysis of large-scale outbreak patterns may reveal local or regional clusters of populations that fluctuate in synchrony as a result of being well-connected by dispersal corridors or having similar climates. A lack of synchrony between clusters might be due to a lack of teleconnectivity between clusters. Even if specific testable predictions can not be formulated beforehand, it is expected that high-resolution pattern analysis will reveal something insightful about the nature of outbreak cyclicity and the effects of forest fragmentation on outbreak patterns.

The specific objectives of this chapter are:

(1) to identify spatial and temporal schemes for simplifying outbreak pattern-sequences for communication and interpretation;

(2) to quantify and characterize the joint spatiotemporal component of the total spatiotemporal variation in outbreak disturbance patterns;

(3) to procure additional evidence that forest tent caterpillar outbreak is the major disturbance affecting aspen growth in Alberta;

(4) to explore the relationship between landscape structure and meso-scale patterns of outbreak asynchrony.

In general, it has been suggested that spatially explicit models are valuable for studying the effects of habitat fragmentation on metapopulation dynamics. Most ecologists agree that space is an important part of ecological interactions; however, it does not follow that a spatially explicit method is necessarily more powerful. Spatially explicit theory has not yet proven to be any more powerful than classical, spatially implicit theory in explaining observed dynamics of real populations. So, while the application of spatiotemporal ecological theory to field biology may be an important question (Kareiva 1990), a more basic question is whether it is at all relevant in the first place. Given the complexity and expense of building and testing spatially explicit population models, this may be one of the most critical issues in population ecology today. As such, the broader goal of this study is to evaluate the general merit of modern spatiotemporal ecological theory in understanding the nature and cause of insect outbreaks - using the forest tent caterpillar as a model system. If the theory is valuable in the case of the forest tent caterpillar, it is likely to be valuable in other instances as well.

6.2 Methods

6.2.1 Outbreak disturbances revealed in aspen ring width chronologies

Chapter three presented detrended trembling aspen (*Populus tremuloides* Michx.) ring width chronologies for 246 stands located in nine municipalities across northcentral Alberta. Stands were aggregated in the form of a 3x3 grid covering 93 500 km^2, and 128 of these stands were evenly distributed over a 420 km^2 area immediately southeast of Cooking Lake, which is located near Edmonton, on the southcentral part of the provincial grid (Fig. 2.1). The longest stand-wise chronology, which came from Whitecourt, extended back to 1837, and the shortest municipal chronology, which was assembled from stands at Frog L., began in 1917 (Fig. 2.3).

6.2.1.1 Animation

Detrended aspen ring widths for each year from 1900-1998 were mapped at provincial and municipal scales and these were animated in order to inspect visually spatiotemporal patterns of growth across each grid (appendix two). Results can be viewed at the url: http://www.biology.ualberta.ca/roland.hp/cooke/anim.html. The animations revealed substantial asynchrony at the provincial scale and slight asynchrony at the municipal scale, suggesting a more quantitative spatiotemporal analysis was worthwhile.

6.2.1.2 Standardization

Preliminary examination of spatiotemporal variation in detrended aspen growth rates indicated unusually high growth rates in certain plots and in certain years, and spatial differences in growth rate means and variances. The first effect was particularly clear on the local grid with regard to unusually high growth at stand #71 in 1961 and 1973 after prolonged outbreaks from 1956-1960 and 1964-1971. The second effect was clear in the lack of distinct coherence at Fort McMurray on the provincial grid.

In order to reduce the impact of growth anomalies (and thus enhance the variation due to periodic growth cycles) each aspen ring width chronology was normalized. Thus purely spatial variation in mean growth rates due to genetic and environmental factors was virtually removed. More importantly, any static spatial patterns in growth reduction that might be associated with gradients in outbreak severity were also removed. Consequently, the data could be used only for investigating temporal and joint spatiotemporal variation in patterns of disturbance impacts.

6.2.1.3 Interpretation

6.2.1.3.1 Removal of drought effects

As defoliation by forest tent caterpillar (*Malacosoma disstria* Hbn.) is the single biggest factor determining aspen growth rates (Hogg 1999), animated patterns of aspen growth are largely indicative of patterns of forest tent caterpillar outbreaks. Aspen growth over the Cooking L. municipality, however, is strongly related to large-scale fluctuations in seasonal precipitation, and this introduces an additional climatic signal into the pattern of aspen growth (chapter two). The magnitude of drought effects across the rest of the province is weaker (chapter three), but can not be ascertained with as much certainty, so removal of such effects was not attempted.

6.2.1.3.2 Inferring outbreaks from patterns of disturbance

In the absence of evidence to the contrary, episodes of reduced aspen growth should not be assumed to be outbreak-caused. Chapter two showed that false inference of outbreaks from aspen ring width chronologies should be a serious concern on the municipal grid. Chapter three showed this should be less of a concern across the provincial grid, except for years prior to 1957, when aerial defoliation maps were not available to corroborate the occurrence of outbreaks. Accordingly, episodes of reduced aspen growth were initially categorized as generic "disturbances".

Each disturbance was examined for associated joint spatiotemporal structure, which would provide additional assurance the disturbance was due to insect outbreak.

The rationale was as follows. Supposing the only factors capable of large-scale aspen growth reduction are drought and defoliation, the fact that drought is not a spreading process suggests that the independent effects of drought and forest tent caterpillar defoliation on aspen growth might be distinguished by partitioning disturbance-caused growth variation into temporal and spatiotemporal components. For example, a joint spatiotemporal component should arise only from a spreading process, such as insect outbreak. A temporal component might or might not include defoliation effects, depending on the scale of outbreak synchrony, which is not known beforehand.

Whereas the temporal analyses of chapters two and three did not address the joint spatiotemporal component of disturbance variability, the current study sought to strengthen the reliability of outbreak inferences by quantifying the joint spatiotemporal structure of disturbance. Once a significant joint spatiotemporal component of variation was revealed in close association with a particular disturbance, an insect outbreak could be more safely inferred, and the disturbance was then categorized specifically as an "outbreak". The greater the magnitude of the joint spatiotemporal variation and the closer the association with a major disturbances, the more confidence one has that a particular disturbance is outbreak-caused.

Because the inferential process is gradual and probabilistic, it is sometimes useful to refer to an ensemble of episodes as a series of "outbreak disturbances", indicating some uncertainty whether all the disturbances are entirely due to insect outbreak. These distinctions may seem confusing at first, but they accurately depict the uncertainty in inferring outbreaks from dendrochronological data. It also serves as a reminder that outbreak dynamics are not being deduced directly from population census data.

6.2.2 Data analysis

All analyses were conducted with the R statistical package, version 1.2.1 (Ihaka & Gentleman 1996, Hornik 2001).

6.2.2.1 Distance-dependent synchrony decay

To determine the spatial scale of synchrony breakdown, distance-dependent synchrony functions were estimated for stand-level provincial and municipal data. The temporal cross-correlation was computed for each pair of stand-wise aspen ring width chronologies across the provincial grid, and this was plotted as a function of distance between plot-pairs (*e.g.* Ranta *et. al.* 1997). Recall a similar exercise based on municipal chronologies showed that synchrony did decay over hundreds of kilometres (Fig. 2.26). This analysis, however, was too poorly resolved to indicate whether there was a threshold distance at which macro-scale synchrony suddenly broke down. By using individual stand-wise chronologies, this parameter could be estimated more precisely. Using 154 stand-wise chronologies spanning the period 1936-1994, synchrony-decay functions were computed for each of the nine municipalities and for the whole province. Thus the provincial synchrony decay function comprised 154 x 153 ÷ 2 = 11 781 data points.

Synchrony decay functions are familiar and useful indicators of distance-dependent synchrony breakdown, but they do not reveal precisely where and when and how synchrony breaks down. This is not an important issue in macro-scale synchrony breakdown where the pattern and mechanism of breakdown are both simple, but it is a fundamental aspect of meso-scale synchrony breakdown, for the pattern and causes of asynchrony might vary for different locations and breakdown may be transient (*e.g.* Ranta *et. al.* 1997). A correlation coefficient is a weak descriptor of such complex structure (Cooke 1998) and there is also no good reason for examining populations in a pairwise manner.

6.2.2.2 Non-linear scaling of outbreak periodicity

The influence of meso-scale synchrony breakdown on the apparent cyclicity of outbreak disturbances was determined by comparing spectral properties of mean municipal chronologies to those of individual stand-wise chronologies within each municipality. Here the goal was to determine if decadal periodicity in municipal disturbances was due to linearly averaged synchronous decadal cycles at the stand-level or if it was a non-linearly scaled emergent property (*e.g.* Chesson 1998) of non-synchronized cycles of various wavelengths. Chapter three showed that each of the mean municipal chronologies was marked by clear decadal outbreak disturbance cycles (Fig. 3.8), but this analysis did not address meso-scale dynamics among stands within municipalities.

6.2.2.3 Spatiotemporal cluster analysis

Cluster analysis was used to determine if, across the province, there were spatial groups of stands where outbreak disturbances covaried similarly in time. The *k*-means clustering algorithm was used to define a single partition of nine clusters of stands that exhibited coherent outbreak patterns. After mapping stand-clusters, these were aggregated into three latitudinal regions.

If each municipality constituted a unique ecoclimatic region, then outbreaks might be expected to behave differently in each municipality. Under this null model, the nine municipal chronologies presented in Fig. 3.2 would constitute the most parsimonious partitioning of regionalized province-wide outbreak patterns. For this reason, nine clusters was chosen as the stopping point for the clustering algorithm.

6.2.2.4 Spatiotemporal factor analysis of outbreak patterns

The province-wide set of aspen ring width chronologies was analysed for coherent spatiotemporal structure by using rotated factor analysis. The goal here was to identify regionalized or punctuated structure in disturbance patterns. Regionalized structure refers to the tendency for spatial clusters to co-vary in time. Punctuated structure refers to the tendency for temporal frames to co-vary in space.

A brief introduction to factor analysis of spatiotemporal ecological data using rotated principal components is given in appendix three because a review of the technique is beyond the scope of this chapter. The works of Richman (1986) and White *et. al.* (1991) provide the foundation for the method, including terminology and algorithms. Meko *et. al.* (1993) show how the technique can be used to uncover spatiotemporal patterns of coherence in large-scale, long-term tree-ring data. All three papers are essential reading.

6.2.2.4.1 Outbreak patterns on the provincial grid

Province-wide disturbance sequences were examined using temporal (T-mode) factor analysis on 154 chronologies covering the 59-year period from 1936 to 1994. Pairwise plots of factor loadings were used to determine whether disturbances exhibited simple temporal structure. Nine factors were extracted because there were nine municipalities and roughly nine large-scale disturbances. With more stands than years, an S-mode analysis could have been conducted by sub-sampling fewer than 59 stands. This was not considered worthwhile because results would have been redundant with those from cluster analysis.

In using T-mode factor analysis on the full data set, the question was whether there were groups of years in which spatial patterns of disturbance covaried, whether these were organized into punctual anomalies, whether anomalies were simple in spatial pattern, whether anomalies were persistent or transient, and whether they were recurrent or unique. Spatial patterns were expected to be either simple or complex in shape depending on whether disturbance dynamics are mediated more by exogenous large-scale ecoclimatic gradients or stochastic effects and endogenous self-organization. Positive covariance among successive disturbance maps was naturally expected over short time-scales because the probability of drought or insect outbreak in a given year is statistically and functionally dependent on past conditions. Negative covariance was expected over slightly longer time-scales because insect outbreaks can spread. The degree of persistence in spatial modes of patterning is influenced by the strength of dependence of future states on past states and the degree to which disturbances are mediated by static environmental variables. Thus it was expected that individual modes of spatial patterning might vary in persistence depending on the extent to which disturbance dynamics are stochastic.

Solutions were rotated using both varimax and promax (m=4) criteria. Pairwise plots of unrotated and rotated factor loadings were examined to determine whether there was simple temporal structure in the data (appendix three).

Two varieties of simple structure patterning were possible. Individual factors might correspond with: (1) individual disturbance trajectories, each possibly showing unique temporal patterns, or (2) individual disturbance episodes, each possibly showing unique spatial patterns. The former would favour the view that disturbances are regionalized as a result of regionally varying factors. The latter would favour the view that disturbances are governed by stochastic factors.

There are two problems with the analysis of spatiotemporal data when plots are aggregated, as they are on the provincial grid. First, much of the joint spatiotemporal variability will arise from disturbances jumping across gaps between municipalities. If disturbances spread slowly relative to the period of oscillation, then the motion may appear as regionally asynchronous pulses. If they spread very quickly, the motion may appear nearly synchronous. The point is worth mentioning at this early stage because it suggests joint spatiotemporal structures, at the provincial scale, should be referred to more generally as "shifts" in disturbance locations, as opposed to patterns of "spread" or "regional asynchrony". Only with highly resolved data, such as on the municipal grid, is it possible to distinguish spread from regional asynchrony. Second, loading patterns resulting from RPCA can be distorted when plots are highly clustered or unbalanced (Karl *et. al.* 1982, White *et. al.* 1991). Therefore the analysis of province-wide data should be regarded as an exploratory analysis.

6.2.2.4.2 Outbreak patterns on the municipal grid

Factor analysis of 67 of the stand-wise Cooking L. aspen ring width chronologies spanning the period 1929-1995 was used to identify spatiotemporal modes of disturbance patterning. Due to the variable length of aspen chronologies, lengthening the time frame of analysis would have required narrowing the spatial extent, and *vice versa*. Choosing this particular spatiotemporal framing served to equalize the number of chronologies to the number of years of data and this was advantageous for two reasons. First, this provided good coverage of stands across the grid while also spanning the period during which outbreaks could be most reliably confirmed by external sources (*i.e.* aerially mapped defoliation). Second, it allowed for both S- and T-mode analyses to be conducted with minimal adjustments to the source data. The latter requires some clarification.

Eigenanalysis requires there be more observations than variables (Richman 1986). For an S-mode decomposition, there must be more time points than plots, and in T-mode there must be more plots than time points. The only way that a set of data can be decomposed using both modes of analysis is if the source data are reduced in the appropriate dimension. This can be done through arbitrary deletion of some data or through random sub-sampling and systematic re-sampling. For a data matrix with equal spatial and temporal dimensions, the simplest approach is to delete some of the more redundant (*i.e.* less informative) observations.

In S-mode decomposition, a vector of data for a single stand was deleted. In T-mode decomposition, a data vector for a single year was deleted. Thus the results from the S- and T-mode analyses were not perfectly comparable, but the difference in information content was so small that the patterns extracted from either mode were robust compared to the size of this trivial alteration. In other words, neither this year nor this plot were crucial to the overall pattern of spatiotemporal variation. The stand that was removed was stand #30 and the year that was removed was 1929. These data were considered the least reliable because they were particularly noisy.

As on the provincial grid, the number of factors extracted was fixed at nine, which was convenient because this happened to be the number of global disturbances that appeared in the mean aspen ring width chronology over the period 1929-1995. Peak years of disturbance on the municipal grid were: 1937, 1942, 1950, 1957, 1968, 1976, 1982, 1987, 1995, although there may have been as many as twelve disturbances. There is some doubt as to whether additional localized disturbances in 1930, 1960, and 1964 could be called outbreaks. Thus depending on one's definition of what constitutes an outbreak, one might want to include as many as twelve factors in an analysis.

It was not clear *a priori* whether outbreak disturbances at the municipal scale should exhibit the same sort of simple temporal or spatial structure that characterizes many meteorological and climatological processes. To be consistent with the provincial analysis it was deemed worthwhile to determine whether disturbances on the municipal grid could be best summarized and interpreted as regionalized oscillations or as punctuated anomalies. Consequently, solutions for both S- and T-mode decompositions were rotated using varimax and promax (m=4) criteria. In each case pairwise plots of factor loadings were used to determine whether disturbances exhibited simple spatial (S-mode) or temporal (T-mode) structure.

6.2.2.5 Environmental correlation analysis

On the provincial grid, previous analyses revealed that fine-scaled variation in drought was less important than it was on the municipal grid (chapter three). Consequently variation components were not compared to precipitation records. Quantitative forest structure data were not available for the provincial grid, so correlation analysis was not possible here either. However a large-scale forest classification (Fig. 3.1) provided some basis for qualitative interpretation of province-wide outbreak variation components.

On the municipal grid it was expected that some aspen stands would be more vulnerable to drought than others. Therefore correlation analysis was used to compare the temporal factor loadings (scores, in T-mode) to precipitation fluctuations. It was also expected that outbreaks might last longer or have a higher periodicity in fragmented forests. Therefore correlation analysis was used to compare spatial factor scores (loadings, in T-mode) to forest cover measured at a variety of spatial scales (see chapter two for detailed methods of measuring forest cover). Lastly, as elevation might play a consistent role in the spatial pattern of outbreak collapse (Cooke & Roland 2000), correlation analysis was used to compare spatial factor scores (loadings, in T-mode) to altitude.

6.2.2.6 Spectral analysis of temporal factor elements

Spectral analysis was used to determine if any of the temporal factor loadings/scores exhibited periodic components that were linked to landscape attributes. We specifically wanted to know if outbreaks were more frequent in fragmented forests.

6.3 Results

In presenting the results of the spatiotemporal factor analyses, frequent reference is made to forest regions, landscape types, and place names to help describe notable patterns of variation. Geographic details can be found in provincial and municipal maps shown in Fig. 2.1, Fig, 2.2, and Fig. 3.1.

6.3.1 Animation of disturbance patterns

6.3.1.1 Weak synchrony on the provincial grid

Disturbances on the regional grid were not well synchronized, appearing as large-scale anomalies that were only vaguely discrete. They were sufficiently spatiotemporally coherent that 8 province-wide traveling waves could be identified and these occurred in pulses covering the following years: 1900-1908, 1913-1920, 1922-1933, 1937-1944, 1947-1959, 1962-1969, 1977-1982, 1986-1989. These waves of disturbance did not exhibit any obvious, consistent directionality.

At each of the municipalities, outbreaks appeared to be fairly well synchronized among stands within municipalities, as was observed on the Cooking L. municipal grid. It seemed outbreaks were fairly well synchronized at 100-400 km^2 but that synchrony broke down at around 10000-40000 km^2. The most notable examples of meso-scale asynchrony occurred at Whitecourt and Drayton Valley, where outbreaks in each municipality appeared to shift between stands in the east and those in the west.

6.3.1.2 Moderate synchrony on the municipal grid

Visual inspection of animated patterns of aspen growth on the municipal grid revealed that disturbances tended to occur every 5 to 7 years. Disturbances were fairly well synchronized, although the presence of some obvious spatiotemporally lagged effects suggested they were probably not due to drought (which would not exhibit lagged behaviour), but to a meso-scale process such as insect defoliation. Meso-scale patterns of asynchronous flow were especially obvious during outbreaks spanning the periods 1923-1930, 1956-1960, 1986-1988, and 1990-1995. In contrast, severe disturbances in 1949-1950 and 1968-1969 were remarkably coherent.

The spatiotemporal progression of individual disturbance episodes can be qualitatively generalized as follows. In the first year, pockets of disturbance tended to appear in a few isolated plots simultaneously and these tended to act as nucleation foci. In the second year, the disturbance would expand from these points to cover much, but not all of the grid. In the third year, it reached its maximum extent and showed grid-wide gradient patterns that also included some small-scale patchiness. As the main part of the disturbance collapsed in the fourth year, new disturbances arose on the portion of the grid that had not yet been disturbed. This new disturbance tended to persist for a year or two and would often disappear just as the next disturbance cycle was beginning on yet another part of the grid, in the fifth to seventh year.

Disturbances had a grid-wide duration of 3-4 years but within most stands they persisted for only 1-2 years. There was some spatiotemporally lagged nucleation and spread. Disturbance spread rates were, however, sufficiently rapid that disturbances appeared as fairly synchronous, spatially heterogeneous pulses. Individual disturbances tended to cover more than half of the grid such that many stands experienced consecutive episodes. Some stands experienced all episodes, but to varying degrees. Disturbances often abated before covering the entire grid. The best example is the chain of localized disturbances from 1950 to 1970. The 1949-1950 episode, which was stronger in the east than in the west, failed to spread westward in subsequent years. The 1956-1958 episode, which was strongest in the east, failed to attain the same level of impact as it spread northward in subsequent years. The 1968-1969 episode, which attained its maximum impact in the north, failed to spread to the south and to the east in subsequent years.

Generalization much beyond this is not possible because each individual disturbance seemed to develop in its own unique way. Nucleation points changed position. Disturbances did not spread in a consistent direction. The spatial pattern and the extent of disturbance varied among episodes, as did the severity of impacts. Notably, episodes in 1937, 1964 and 1977 were widespread, but not as severe or as localized as in episodes such as 1942, 1957, 1968, and 1987. Yet these events were undoubtedly due to a meso-scale disturbance such as insect outbreak, because they were associated with spatiotemporally lagged patterns of development in the years both preceding and following. In contrast, the disturbance of 1972, which was as weak and as uniform as disturbances in 1937, 1964, and 1977, occurred suddenly and was not obviously associated with a prolonged spatiotemporally lagged developmental cycle. Reduced growth in 1972 therefore may not have been a result of forest tent caterpillar outbreak, but there is no independent proof to support this hypothesis.

6.3.2 Synchrony decay

Among the 246 stands on the provincial grid, outbreak synchrony decayed smoothly as a function of distance between pairs of stands (Fig. 6.1a). Correlations between pairs of stand-wise chronologies dropped to zero at separation distances of 200-400 km. Within municipalities, correlations also decayed smoothly as a function of distance, although the rate of decay was sufficiently low that in no municipality did the correlation decline to zero (Fig. 6.1b-i). The largest declines in synchrony were observed in Whitecourt and Drayton Valley (Fig. 6.1e, h), where western stands were located in the continuously forested landscape of the boreal mixedwood and eastern stands were located in the fragmented landscape of the aspen parkland (see Fig. 3.1). The rate of decay within continuously forested western clusters and fragmented eastern clusters did not differ (Fig. 6.2)

6.3.3 Non-linear scaling of outbreak periodicity

Outbreaks were decadally periodic both at the level of the whole municipality and the individual stand (Fig. 6.3). Thus decadal periodicity in municipality-wide outbreaks was not an emergent property of higher- or lower-frequency outbreaks at the stand level. Notably, however, the decadal spectral peak was stronger in the spectrum of the mean municipal chronologies than in the mean spectrum of individual stand-wise chronologies. This was especially obvious in Whitecourt and Drayton Valley (Fig. 6.3d, g). This suggests slightly non-linear scaling effects (*sensu* Chesson 1998) in the scaling of outbreak periodicity from the level of stands to municipalities. This was a product of the weak pattern of sub-decadal asynchrony between stand clusters and decadal synchrony among clusters that was exhibited in the animated data.

6.3.4 Cluster analysis

Cluster analysis showed that there were groups of stands where disturbances covaried similarly and that the grouping was spatially oriented. Using nine clusters, three major regions of distinct dynamics were revealed: (1) aspen parkland, which comprised clusters 1, 5, 6 and 8, and was located on the southern portion of the provincial grid; (2) mixedwood transition, which comprised clusters 2, 3 and 7, and was located centrally; (3) northern boreal, which comprised clusters 4 and 9, and was located on the northern part of the provincial grid (Fig. 6.4).

Although some disturbances spanned all three regions (*e.g.* 1941-1943, 1962-1964, 1980-1982), each region nonetheless exhibited its own particular temporal pattern of disturbance (Fig. 6.5). For example: (1) disturbances in 1950, 1957, and 1995 were centered on the aspen parkland; (2) disturbances from 1977-1983 were particularly severe and long-lasting in the mixedwood transition; (3) disturbances had minimal impact in the boreal region except during 1981-1982. Notably, stands in the fragmented landscapes of Drayton Valley and, to a lesser extent Whitecourt, exhibited disturbance patterns that were more closely related to patterns at Cooking L. (more than 120 km to the East) than to patterns in nearby continuously forested landscapes (less than 50 km to the West). This was evidenced as a distinction between cluster 7 (continuously forested) and cluster 8 (fragmented) (Fig. 6.6), which was driven by disturbance asynchrony during the periods

1941-1964 and 1986-1990. Also noteworthy, stands at Dixonville could be divided into three sub-groups, depending on whether disturbances there were better synchronized with disturbances of the parkland, central or boreal regions (clusters 4, 2, 8 respectively).

The three major regional clusters differed significantly in the regularity and frequency of outbreaks. Disturbances were more highly periodic and more frequent in the parkland, less periodic and less frequent in the boreal, and intermediate in the mixedwood transition (Fig. 6.6). Notably, disturbances at cluster 6 and cluster 7 were similar in regularity and periodicity (Fig. 6.6). However individual disturbances differed slightly in magnitude (*e.g.* 1946, 1958, 1969, 1982) and phasing (*e.g.* disturbances occurring earlier in cluster 6 (1950, 1975, 1987) than cluster 7 (1952, 1978, 1989)) (Fig. 6.6).

6.3.5 Spatiotemporal factor analysis

6.3.5.1 Provincial grid

At the provincial scale, cluster analysis showed there was some regionalized coherence among stands in temporal patterns of aspen growth. But no one simple spatial partition could cleanly delineate zones of high synchrony. Even with a partition of nine regionally synchronized clusters, coherence within clusters was fairly low due to a significant joint spatiotemporal component of variation.

6.3.5.1.1 T-mode analysis

T-mode factor analysis showed that 17.3% of the total spatiotemporal variation in disturbance patterns could be explained by the first factor, representing the persistent tendency toward low-frequency disturbance. Factor one scores were strongly positive at Cooking L. and decreased to strongly negative toward the north (Fig. 6.7a), indicating a tendency for disturbances to be out of phase between these regions. Factor one loadings (Fig. 6.8a) were highly periodic, with a dominant spectral peak at 10.0 years (Fig. 6.9a). Thus there appears to be a weak, but persistent tendency for decadal disturbances in the south to be poorly synchronized with those in the north, which is consistent with results from cluster analysis.

Factor two, accounting for 5.1% of the spatiotemporal variation, was related to the weakly persistent trend for outbreaks in recent decades to shift from east to west across the province over a five-year period (Fig. 6.7b). Major contributing disturbances here were the decadal outbreaks of 1976 and 1987, which lasted from 1974 to 1978 and 1985 to 1989 respectively (Fig. 6.8b).

Similarly, factor three, accounting for 4.8% of the spatiotemporal variation, reflected the weakly persistent tendency during earlier decades for outbreaks to initiate in the northwest and shift to the northeast (Fig. 6.7c). The major contributing disturbance here was the decadal outbreak of 1949 (Fig. 6.8c), which emerged first in 1946 in the northwest, peaked in the southwest, moved to the northeast in 1952, and was resuscitated in the northwest in 1956 before collapsing in 1957, at the same time a new round of outbreaks began elsewhere in the province.

Like factor three, factor four, which accounted for 3.8% of the spatiotemporal variation, related to asynchrony during earlier decades (Fig. 6.7d). And like factor two, factor five, which accounted for 3.6% of the spatiotemporal variation, related to asynchrony during more recent decades (Fig. 6.9e). The only difference between factors two and three *versus* factors four and five is that the latter emphasized persistent asynchrony in the super-decadal frequency range. Thus the spatial modes of variation associated with factors four and five (Fig. 6.8d,e) were a little more persistent.

Each of the four remaining factors explained less than 3.5% of the variation and related to higher-frequency (Fig. 6.9f-i) asynchrony between regions (Fig. 6.7f-i). This asynchrony was persistent and was not dominated by spatiotemporal variability associated with any one particular outbreak (Fig. 6.8f-i).

Interpretation much beyond this was difficult. First, orthogonality implies that the lesser factors must be interpreted marginally, especially with respect to factor one. And because factor one reflected latitudinal asynchrony, these lesser factors likely represented different effects in different areas. Second, and in addition, subdomain instability is a major problem with unrotated solutions (Richman 1986). Third, and consistent with these observations, the unrotated decomposition did a poor job of extracting simple temporal structure in the data, as evidenced by pairwise plots of factor scores, which showed a lack of clustering along the axes (Fig. 6.10).

6.3.5.1.2 Effect of rotation

Pairwise plots of factor loadings revealed a much tighter clustering of loadings along component axes after promax rotation (Fig. 6.11). The varimax rotation was only slightly less effective in extracting simple temporal structure in disturbance patterns. The two rotations also differed little in the spatial patterns of factor scores and temporal patterns of factor loadings. Results are therefore described for promax rotation only, as this rotation was slightly more effective in extracting simple structure.

After promax rotation, temporal loading patterns for each of the factors was dominated by one or two high-amplitude, transient pulses (highlighted in Fig. 6.12), indicating negative spatial covariation between specific disturbance patterns (Fig. 6.13) over a 2- to 5-yr interval. In all, fifteen such pulses were revealed among the nine factors, some of these conjoined by a pivot year. Each was closely associated in time and space with at least one spatiotemporally regionalized disturbance, and usually with a second discrete, minor, localized disturbance (Table 6.1). Nine major (1942, 1949, 1957, 1962, 1968, 1978, 1982, 1987, 1994) and ten minor (1940, 1946, 1951, 1953, 1955, 1960, 1965, 1973, 1980, 1990) disturbances could be discerned using these criteria. Thus the provincial periodicity of localized disturbances was 59 years/19 disturbances = 3.1 y, even though the municipal periodicity of municipal disturbances was shown, in chapter three, to be ≈ 10 y. Under this interpretation, it appeared that the emergence and subsidence of regional outbreaks was consistently related to the asynchronous subsidence and emergence of more localized outbreaks elsewhere in the province.

Although individual factors mapped closely to individual localized disturbances, there was some persistent asynchrony associated with some of the factors. As in the unrotated solution, factor one again reflected asynchrony between the parkland and boreal regions (Fig 6.13a) in the decadal frequency range (Fig. 6.14a). Factor two again reflected asynchrony between eastern and western regions (Fig 6.13b) in the decadal frequency range (Fig. 6.14b). Factor three reflected fine-scale, within-municipality asynchrony (Fig 6.13c) in the sub-decadal frequency range (Fig. 6.14c). The amplitude of low-frequency variability in loadings on other factors was negligible compared to the amplitude of single transient pulses (Fig. 6.12d-i). Consequently these series were non-stationary in variance and decadal variability indicated in their spectra (Fig. 6.14d-i) was less meaningful.

6.3.5.2 Municipal grid

6.3.5.2.1 Overview of results

With two analytical modes, three rotations, nine factors, and four diagnostics to discuss (factor loadings, scores, their spectral properties, and their tendency to cluster in pairwise plots), at least 24 multiple-panel plots would be required to completely summarize the results, and then 162 factors would need individual interpretation. Rather than attempt to present all this raw information and verbiage, results from exploratory analyses were distilled into a more manageable form, based on the most notable trends. Given the subjective nature of rotated factor analysis and the danger of over-interpretation, it seemed prudent to focus on major features in the data.

The unrotated S-mode analysis provided a decomposition that was both communicable and interpretable, so these results are described first, and in some detail. Here, individual factors are interpreted in terms of their spectral properties and their relationship to forest structure, elevation and precipitation. Next, the effects of rotation are summarized. Finally, the results from T-mode analysis are described in general comparison to those from S-mode analysis. Here, details are highlighted only where there are major differences in factor interpretation. To provide some coherence to the presentation, environmental correlations for both analytical modes and all three rotations are summarized in a single table (Table 6.2).

6.3.5.2.2 S-mode analysis

6.3.5.2.2.1 Unrotated solution

The first factor from unrotated S-mode analysis of the municipal data accounted for 50.8% of the total spatiotemporal variation in aspen ring widths. Temporal fluctuations in factor one scores (Fig. 6.15a) were identical to fluctuations in the mean municipality-wide aspen ring width chronology (Fig. 2.4c or Fig. 3.2), with fairly smooth transitions from positive values in 1935, 1939, 1947, 1953, 1962, 1973, 1979, 1984, and 1991 to negative values in 1937, 1942, 1950, 1957, 1968, 1976, 1982, 1987, and 1995. The first factor loadings were positive for all stands (Fig. 6.16a), suggesting factor one represented the strong general tendency for episodes of reduced growth to occur synchronously across the grid. Of course, if growth variation had been perfectly synchronized, this first factor would have accounted for all of the spatiotemporal variation.

Synchronized episodes of reduced growth captured in factor one scores were weakly periodic with a 7- to 10-year cycle (Fig. 6.17a). Spatial variation in factor one loadings did not relate to forest structure measured at any spatial scale (Table 6.2). But factor one scores correlated well with precipitation (Table 6.2) in the same way that the mean aspen ring width chronology correlated with precipitation (Fig. 3.4). Thus it is possible that factor one includes some effect of drought in addition to defoliation by forest tent caterpillar outbreak.

With the first factor interpreted this way, the remainder of the spatiotemporal variation in aspen ring widths (49.2 %) could be interpreted as additional variation due to noise and to poorly synchronized disturbance unrelated to drought. Factors two to nine accounted for 20.5% of the total spatiotemporal variation, leaving 28.7% unaccounted for by the first nine factors. The fact that scores from factors two to nine were unrelated to precipitation (Table 6.2) supports the view that these factors are related not to large-scale drought but to forest tent caterpillar outbreak asynchrony. Thus, each of factors two to nine can be broadly interpreted as a tendency for outbreaks to deviate from the mean temporal trajectory already described and analyzed (chapter two). In conjunction with the large portion of variation accounted for by factor one, this implies that the decomposition obtained from unrotated S-mode analysis offers a highly communicable summary of the animated data.

To interpret each of factors two to nine, it will help to consider two things: the expected form and the expected magnitude of joint spatiotemporal variability. First, the joint spatiotemporal variation not captured in factor one could be revealed in a variety of forms, from: (1) anomalous localized infestations unrelated to the major disturbances in 1937, 1942, 1950, 1957, 1968, 1976, 1982, 1987, and 1995, to (2) focal epicentres, gradients and refugia resulting from the nucleation, spread, and heterogeneous collapse of any of the widespread outbreaks captured in factor one. Second, if the 49.2% of spatiotemporal variation not explained by factor one were divided equally among the nine disturbances revealed in factor one, then the expected joint spatiotemporal variability associated with each disturbance would amount to 5.5% of the total. This provides a meaningful denominator for scaling the proportions of variation explained by each of factors two to nine.

Factor two, which accounted for 4.0% of the total spatiotemporal variation, emphasized a smooth and rapid transition between negatively covarying patterns of aspen growth from 1990 to 1994 (Fig. 6.15b). The map of factor two loadings (Fig. 6.16b) shows that, in addition to the synchronous widespread disturbance from 1992 to 1995 revealed in factor one (Fig. 6.15a), there was a substantial component of spread of outbreak from the south and east into the central and western parts of the grid. Coupled with the knowledge that aspen growth rates generally shifted from high in 1990 to low in 1994 (Fig. 6.15a), this suggests the disturbance was due to a tent caterpillar outbreak, and that this outbreak began in the south and east and quickly spread to a central position where it peaked in 1994 before attaining much impact in the south and east. This pattern of spread was weakly related to forest structure measured at 106m ® = 0.28), but was unrelated to forest structure measured at any other scale (Table 6.2). Thus it appears that the 1992-1995 outbreak was initiated in 1990 from focal epicentres located on the fringe between forested and fragmented landscapes. Other disturbances did not exhibit the same pattern of initiation, otherwise they would have been evidenced in the temporal loadings on factor two. Note the decadal periodicity exhibited in the spectrum of factor two scores (Fig. 6.17b) is practically meaningless because factor two scores are non-stationary due to the high-amplitude transient pulse from 1990 to 1994.

Factor three, which accounted for 3.4% of the total spatiotemporal variation, emphasized a smooth and moderately rapid transition between negatively covarying patterns of aspen growth from 1952 to 1956 (Fig. 6.15c). Neither of these were general years of disturbance, so the marginal interpretation with respect to factor one is not as simple as it was for factor two. The negative spatial covariance here encapsulates two features sharing a common pattern: (1) the manner in which the 1949-1950 disturbance abated asynchronously, and (2) the manner in which the 1957-1960 disturbance emerged asynchronously. The first disturbance began abating in 1950 across the southwest portion of the grid, and this is precisely where the second disturbance began in 1956 (Fig. 6.16c). Factor three spatial loadings were unrelated to forest structure, but were weakly related ® = 0.33) to altitude (Table 6.2). Thus it appears that: (1) the 1950 disturbance was outbreak-related; (2) this outbreak collapsed first on the higher, southwest portion of the grid; (3) the effects carried over into the next outbreak sequence in the late 1950's; (4) no other disturbances exhibited the same altitudinal mode of spatiotemporal patterning (although loadings from 1988-1994 also indicated a weak tendency for the abatement of the 1987 disturbance to follow a similar progression). As with factor two, decadal periodicity in the spectrum of factor three scores (Fig. 6.17c) is practically meaningless because factor three scores are non-stationary due to the one pulse from 1952 to 1956 and the lesser pulse from 1988-1994.

Factors four through nine resembled factors two and three in that factor scores exhibited brief, high-amplitude pulses (Fig 6.15d,e,f,g,h,i). But at the same time, scores for these factors were not entirely dominated by single pulses. Due to their stationarity, scores for factors four through nine were more like factor one scores. In other words, while factors two and three emphasized the transient, anomalous side of three large-scale decadal outbreaks, factors four through nine increasingly highlight persistent, high-frequency phenomena that are not so obvious upon casual inspection of the animated data.

Factor four, which accounted for 3.3% of the total spatiotemporal variation, was distinct in its high-frequency volatility in factor scores (Fig. 6.15d). Factor four loadings contrasted a northeastern arm on the grid with a southeastern pocket (Fig. 6.16d). It was over the northeastern arm where the 1987 outbreak first became obvious, in 1985/1986, and first collapsed, in 1988, leading to an early recovery of aspen growth rates in 1989/1990, which subsequently dropped to normal levels in 1991/1992. Meanwhile aspen growth elsewhere on the grid was recovering from prolonged outbreak into 1989. The 5-yr periodicity in factor four scores (Fig. 6.17d) was not due solely to the two high-amplitude pulses from 1986 to 1988/1989 and 1991 to 1993/1994, but it was not compromised by them either. The spatial loadings were weakly-related ® = 0.26) to forest cover measured at 425m (Table 6.2), which reflects the association with the largely forested and partially fragmented landscape of the Cooking Lake-Blackfoot Grazing Reserve which covers the northcentral sector (Fig. 2.2).

Factor five, which accounted for 2.5% of the total spatiotemporal variation, emphasized an interesting feature of the data set that was weakly related to the early development of the 1987 outbreak and more strongly related to the subsequent spread of this outbreak across the grid (Fig. 6.16e). The 1987 outbreak appears to have initiated in 1984 and 1985 from isolated focal patches concentrated on the east and central part of the grid (Fig 6.16e), where an outbreak finally precipitated in 1986. Upon reaching its maximum extent and impact in 1987, this outbreak spread outward from its epicentre to the west and north over the next two years, while collapsing at its origin in 1988. Notably, the emphasis on the asynchronous emergence and spread of the 1987 outbreak in factor five was accompanied by a similar but smaller component which related to the asynchronous emergence and spread of the 1942 outbreak. These outbreaks shared a similar pattern of early development. In 1941, several patches on the west and central parts of the grid were not defoliated and these were also largely not defoliated in 1942, when the outbreak reached its largest extent. As the outbreak generally subsided in 1943 and aspen growth recovered in the east, the outbreak moved into the formerly non-defoliated patches in 1944 and 1945. These lingering outbreak refugia were closely associated with a larger, but localized outbreak that subsequently emerged in 1946. This outbreak registered as only a weak disturbance in the mean ring width chronology. Factor five loadings were uncorrelated with forest structure, suggesting that the 1944 and 1984 refugia were not related to the degree of local forest fragmentation. Factor five scores were fairly periodic with a 10-yr cycle (Fig. 6.17e) suggesting a persistent, rather than a transient refuge effect.

Factor six, which accounted for 2.1% of the total spatiotemporal variation, exhibited a complex pattern of fluctuation in temporal scores (Fig. 6.15f), which included decadal and sub-decadal components (Fig. 6.17f), and a simple gradient pattern in spatial loadings (Fig. 6.16f), which was related to forest cover measured at the larger spatial scales (Table 6.2), especially at 1700m ® = -0.38). There was no one disturbance that dominated the fluctuations in temporal scores. The most notable deviations from factor one scores included a dip in 1960, when the 1957 grid-wide outbreak had largely abated, and a peak in 1969, when a grid-wide disturbance had reached maximum intensity. Similar asynchrony with factor one was also evident during the early phase from 1929 to 1957. Thus factor six seemed to represent a general tendency for the first four sub-decadal outbreaks (1930, 1937, 1942, 1950) to have a weaker impact in the highly fragmented landscape.

Factor seven scores deviated from factor one scores with regards to the timing and/or intensity of disturbances in 1937, 1950, 1969, and 1987 (Fig. 6.15g). Along a central north-south axis (Fig. 6.16g), aspen growth was lower than average in 1935/1936, but higher than average in 1937/1938; it was higher than average in 1950, but lower than average in 1951; it was higher than average in 1969, but lower than average in 1973; it was lower than average in 1983/1984, but higher than average in 1986/1987. Thus it appears that along this axis the negative effects of large-scale defoliation were not as severe and the delayed positive effects were also not as large. Factor seven scores were not highly periodic (Fig. 6.17g) and spatial loadings were unrelated to forest cover (Table 6.2). It appears, then, that factor seven distinguishes areas where impacts of four outbreaks happened to be damped. That outbreaks in 1942, 1957 and 1982 did not exhibit a similarly shaped damping gradient suggests the effect may not be persistent.

Like factor seven, factors eight and nine each accounted for less than 2% of the total spatiotemporal variation. Factor eight and nine loadings showed a patchy/gradient structure (Fig. 6.16h,i) that was unrelated to forest cover (Table 6.2). Unlike any of the other factors, factor eight and nine scores were not dominated by any one high-amplitude pulses (Fig. 6.15h,i). They were not highly periodic (Fig. 6.17h,i). These factors appear to represent natural outbreak stochasticity or sampling error.

In summary, the picture painted by the unrotated S-mode analysis suggests that much of the joint spatiotemporal variation in aspen growth was transient, anomalous variability in very close association with the nine major grid-wide outbreak disturbances of 1937, 1942, 1950, 1957, 1968, 1977, 1982, 1987, and 1995. A small portion of joint spatiotemporal variation was accounted for by highly persistent patterns of asynchrony in weak association with these major disturbances. Comparatively little of the joint spatiotemporal variation was due to localized disturbance anomalies occurring between these major pulses.

6.3.5.2.2.2 Effect of rotation

Pairwise plots of factor loadings indicated that unrotated decomposition was largely unsuccessful in extracting simple spatial structure (Fig. 6.18). Promax rotation was somewhat more successful (Fig. 6.19), but not nearly as much as it was on the provincial grid (Fig. 6.11). Varimax rotation was even less successful in extracting simple spatial structure; however, patterns in temporal loadings and spatial scores did not differ much between the two rotations. Consequently results are presented for promax rotation only.

As a non-orthogonal rotation, the promax rotation produced factor scores that shared many features with the unrotated factor one scores (Fig. 6.20). The primary effects of rotation on factor scores are best summarized by considering three kinds of differences with respect to factor one scores: (1) variation in disturbance weights; (2) variance stationarity; (3) spectral enhancement in a particular frequency range.

Factor one emphasized variation in impacts of the 1987 outbreak during the years 1986-1988, and seemed also to reflect increasing asynchrony of disturbance (Fig. 6.20a) between the continuously forested landscapes in the south and north and the fragmented landscapes of the east and west (Fig. 6.21a) - this particularly with respect to decadal disturbance (Fig. 6.22a). Spatial loadings were, however, uncorrelated with forest cover (Table 6.2).

Factor two emphasized an early emergence of the 1957 disturbance in 1956 and variation in peak impacts in 1957, as well as variation in 1969 impacts, and delayed abatement the 1987 disturbance in 1989 (Fig. 6.20b), all of which were organized along a rough east-west gradient that included some patchiness (Fig. 6.21b). Spatial loadings were correlated with altitude ® = 0.37) but were unrelated to forest cover (Table 6.2). Thus the early emergence of these disturbances was associated with the higher land to the west and northwest. Temporal scores for factor two were also more strongly related to precipitation ® = 0.47) than were scores for any other factor, so it is possible that this factor reflects spatial variation in vulnerability to drought.

Factor three emphasized three effects: (1) asynchronous decline of three disturbances, (2) increasing high-frequency asynchrony, and (3) implosion of the 1990-1995 outbreak. First, localized disturbances in 1944, 1952, and 1960 (Fig. 6.20c) were associated with large-scale disturbances in 1942, 1950 and 1957. These three pockets of residual disturbance were arranged in a triangle (Fig. 6.21c), in no relation to forest cover or altitude (Table 6.2). Second, the variance of factor scores seemed to increase over time, indicating enhanced asynchrony, particularly in the sub-decadal frequency range (Fig. 6.22c). Third, the 1992-1995 outbreak appeared to begin as the 1986-1989 outbreak ended, when, in 1990, disturbance pockets appeared in a circular, target-like arrangement around the grid periphery and outside the triangle of positive loadings (Fig. 6.21c). This outbreak coalesced around the grid centre in 1995 while collapsing at the periphery.

Factor four emphasized two effects: (1) spatial variation in the early abatement of the 1957-1960 and 1986-1989 disturbances in 1959 and 1987 respectively, (2) spatial variation in the magnitude of localized disturbances in 1940, 1964 and 1981-1982 (Fig. 6.20d). This particular weighting of disturbances led to strong sub-decadal periodicity in factor scores, particularly in the 4- to 6-yr range (Fig. 6.22d). The spatial loadings revealed this persistent, high-frequency asynchrony was manifest spatially as a distinct triangular patch of positive loadings in a matrix of neutral loadings (Fig. 6.21d). The loadings were unrelated to forest structure (Table 6.2), but the triangular patch of positive loadings lay just north and east of the grid centre, at the junction of the four major landscape polygons, and included the area immediately surrounding Hastings Lake (Fig. 2.2).

Factor five scores emphasized localized disturbances in 1942-1943, 1966-1967, and 1976-1981, but de-emphasized regional disturbances surrounding 1937, 1964, and 1987 (Fig. 6.20e), resulting in a strong decadal pattern of disturbance (Fig. 6.22e) that contrasted sharply with factor four and unrotated factor one. Although factor five loadings were unrelated to forest structure (Table 6.2), factor five loaded positively on the continuously forested area northeast of Hastings Lake, negatively on the continuously forested area to the southwest, and neutrally on the fragmented portions of the grid.

Factor six scores were dominated by spatial variation in disturbance impacts in 1949-1951 and 1986-1987 (Fig. 6.20f) which were strongest in the highly fragmented landscape of the southeast (Fig. 6.21f), thus explaining the negative correlation with forest cover measured at 850m ® = -0.32).

Factor seven was dominated by the spatial variation in the abatement of the 1957-1960 outbreak, which lingered on for an extra year or two (Fig. 6.20g) along a central north-south axis (Fig. 6.21g).

Factor eight and nine scores seemed noisier (Fig. 6.20h,i) and were less periodic (Fig. 6.22h,i). And although each accounted for less than 3% of the total spatiotemporal variation, these factors illustrated a different kind of between-episode spatiotemporal asynchrony not evidenced in the other factors. To visualize these it is necessary to locate

6-8 year trends in factor scores where smooth changes from strongly positive to strongly negative (or *vice versa*) occur in association with two separate grid-wide disturbance pulses separated by the same amount of time. Factor eight illustrates two such events, from 1935 to 1942, and from 1977 to 1982 (Fig. 6.20h), and factor nine illustrates three such events, from 1965 to 1972, from 1976 to 1982 and from 1988 to 1994 (Fig. 6.20i). These spatiotemporal structures represent the tendency for successive grid-wide disturbance episodes to exert their maximum impact on different parts of the grid - a spatiotemporal exclusion effect. Factor eight reflects a vague east-west exclusion effect on the southern part of the grid, especially focused on two patches on either side of the Ministik Hills Bird Sanctuary (Fig. 6.21h), while factor nine represents a vague east-west exclusion effect on the northern part of the grid, especially contrasting the Cooking Lake-Blackfoot Grazing Reserve with the fragmented landscape surrounding Cooking Lake (Fig. 6.21i). Factor eight loadings were unrelated to forest cover, but factor nine loadings were ® = 0.31).

The apparent noisiness in factor eight and nine scores having been reduced by isolating these exclusionary effects, what remains are additional asynchronous localized anomalies evident in 1961 in factor eight (Fig. 6.20h) and 1954 in factor nine (Fig. 6.20i). There is also evidence of a slow-spreading pattern of localized infestations from 1929 to 1935 in factor eight, which covered the endemic period between grid-wide outbreaks in 1925-1927 and 1936-1938.

In summary, analysis of the non-orthogonal rotated solution reaffirmed that much of the joint spatiotemporal variation in aspen growth was transient, anomalous variability in very close association with the nine grid-wide disturbances of 1937, 1942, 1950, 1957, 1968, 1977, 1982, 1987, and 1995. It also revealed that a small portion of joint spatiotemporal variation was accounted for by weakly persistent patterns of asynchrony in strong association with these major disturbances. It suggested that comparatively little of the joint spatiotemporal variation was due to localized disturbance anomalies occurring between these major pulses, although localized disturbances in 1946, 1954, 1964, 1972 were locally associated with a tendency toward weaker impacts of the major disturbances bracketing them - in 1942, 1950, 1957, 1968, and 1977. These localized disturbances were therefore likely caused by localized forest tent caterpillar infestations, despite their small size and impact. The spatiotemporal patterns of minor disturbances in 1977 and 1982 were tied to one another and to disturbance patterns in 1972 and 1987, suggesting these were caused by localized outbreaks which, for some reason, did not grow into large outbreaks. Similarly, the early development of the 1937 outbreak in 1935 was linked to the pattern of prior infestations through the endemic period of 1929-1931, and to the subsequent pattern of exclusionary outbreak pulses in 1937 and 1942.

Thus there were a total of fourteen localized disturbances with a significant joint spatiotemporal component of variation occurring in close association with a major disturbance. If each of these is truly the result of defoliation by forest tent caterpillar, the periodicity of infestations is 4.8 years. No one group of stands was vulnerable to all fourteen outbreaks, but the area surrounding Hastings Lake showed the highest vulnerability, exhibiting effects from the twelve largest outbreaks. Disturbances in 1954 and 1972 were not focused on that area.

Forest cover was weakly associated with spatial patterns of outbreak asynchrony, through factors six and nine, which accounted for very little of the total spatiotemporal variation. The highest frequency of outbreaks did occur in the area surrounding Hastings Lake, which is highly fragmented and lies between two large areas of continuous forest to the north and to the south. However, other fragmented areas in the east and west did not reveal similar patterns of persistent high-frequency periodicity. On the other hand, these areas did reveal a tendency toward different forms of landscape-related asynchrony, as evidenced in factors three and six. The lowest frequency of outbreaks occurred in the continuous forests of the grazing reserve, but the more highly forested bird sanctuary exhibited a higher outbreak frequency. If forest cover mediates local dynamics, the effects are not obvious here.

6.3.5.2.3 T-mode analysis

6.3.5.2.3.1 Unrotated solution

The unrotated solution from T-mode analysis yielded a decomposition that was neither parsimonious nor particularly interpretable. Loadings on factors one, two and eight were dominated by single pulses, while loadings on factors three, four, five, six exhibited nonstationary periodicity, and loadings on factors seven and nine were stationary in their weak periodicity (Fig. 6.23). Factor three emphasized the emergence of a 12-yr cycle around 1960 (Fig. 6.24c). Similarly, factor four emphasized the emergence of a 10-yr cycle around 1950 (Fig. 6.24d). Factor five emphasized the evolution of a 5- to 6-yr cycle into a 10- to 12-yr cycle around 1950 (Fig. 6.24e). Factor six emphasized the decay of a 5- to 6-yr cycle around 1960 (Fig. 6.24f).

Perhaps notable, factor five scores were weakly positive throughout the fragmented landscape on the western portion of the grid (Fig. 6.25e), accounting for a weak negative correlation ® = -0.26) with forest cover measured at 1700m (Table 6.3). Also, factor six scores were weakly positive along the northeastern and southeastern fringes of the continuously forested landscape (Fig. 6.25f), accounting for a positive correlation ® = 0.31) with forest cover measured at 212m. These two factors together suggest a marginal decay in the pattern of high-frequency asynchrony between continuous and fragmented areas during recent decades. This trend is not a strong one however, because these factor account for only 4.5 and 3.9% of the total spatiotemporal variation. Further, these factors cannot be interpreted in isolation of the others, because they do not reflect simple and independent spatial structures (Fig. 6.25).

The most informative feature of the unrotated T-mode analysis is that none of the factor loadings correlated with precipitation any better than did unrotated S-mode factor one. The strongest correlation ® = -0.29) was found with factor seven (Table 6.3). If drought were a factor that operated independently of any others, at least one of the temporal modes of variation ought to reflect the overall effect of that variable. But this is not the case. No factor scores positively across the grid (Fig. 6.25) and all temporal modes of variation are dominated by low-frequency variation (Fig. 6.23) unrelated to precipitation (Table 6.3).

That factor one did not score positively across the grid also implies that outbreaks, too, are not global municipal phenomena. In other words, not all stands in a municipality are equally likely to be defoliated at a given time. Instead, outbreaks are regionalized over a spatial scale somewhat smaller than the extent of the municipal grid. Indeed, one might use the term "localized" to describe such a small scale of dynamic clustering.

6.3.5.2.3.2 Effect of rotation

The promax rotation was remarkably effective in extracting simple temporal structure, as indicated by pairwise plots of rotated factor loadings (Fig. 6.26). As with previous analyses, varimax rotation was less effective. Patterns of factor loadings and scores did not differ appreciably between the two types of rotations, so results are described for promax rotation only.

The principal feature of the temporal factor loadings was the domination of each by a small number of transient, high-amplitude pulses (Fig. 6.27). Comparing the endpoints of these pulses (highlighted in Fig. 6.27) to patterns in the mean chronology, it is clear that the low end of these pulses typically corresponded to a year of peak global municipal disturbance and the high end corresponded to a temporally different, neighbouring disturbance. Thus the pulses were, on average, 6.0 years in length. These spatiotemporal structures therefore represented the weakly persistent tendency for the maximum impact of successive disturbances to occur on different portions of the grid. Here the spatial mode of exclusion was reflected in maps of factor scores (Fig. 6.28). This exclusionary pattern was similar to the pattern revealed in factors eight and nine of the rotated S-mode analysis (Figs. 6.20, 6.21), but here the pattern was much more obvious. Apparently, promax rotation was more effective in T-mode than in S-mode in extracting simple exclusionary structure.

In all, ten pulses could be identified among the nine factors, and these were linked with fourteen disturbances of varying size and intensity (Table 6.4). Factors one through nine accounted for 45.3% of the total spatiotemporal variation in aspen growth, suggesting that something less than this amount was attributable to grid-wide, sub-decadal disturbance asynchrony. This asynchronous pattern was revealed clearly in a sequence of time-averaged growth maps (Fig. 6.29). By setting the temporal frame boundaries to exclude years of peak growth, individual frames represented the spatial pattern of disturbance, and did so without framing bias. The spatial correlation between successive disturbances was strongly negative, but it damped to zero for non-successive disturbances (Fig. 6.30), meaning that successive outbreak pulses tend to be spatially segregated.

6.4 Discussion

6.4.1 Prominence of insect outbreaks

Each and every major disturbance, whether at the municipal or provincial scale, had associated with it a significant component of joint spatiotemporal variation. If large-scale decadal drought were the major factor limiting aspen growth, then disturbances would not appear to spread from stand to stand or shift from municipality to municipality in this manner. That disturbances consistently display joint spatiotemporal variability over a time scale that is short relative to the period of oscillation helps to confirm the conclusions of chapters two and three: insect outbreaks are the major cause of disturbance in Alberta. Forest tent caterpillar is surely the dominant species contributing to these large-scale patterns.

6.4.2 Optimal partitioning

6.4.2.1 Provincial grid

Outbreaks at the provincial scale were so poorly synchronized and yet sufficiently well-organized that the dynamics are difficult to summarize in a few words. Cluster analysis indicated some outbreak regionalization: the province could be broadly partitioned into parkland and boreal regions. However, subdivision much beyond this tended to mask temporary periods of synchrony across regions and subregions. For example, the eastern/fragmented and western/continuous stand-clusters at Whitecourt and Drayton Valley were sometimes well-synchronized, sometimes partially synchronized, and sometimes not synchronized. As a second example, regionalized outbreaks were frequently associated with localized infestations outside the primary region of outbreak, but the location of these isolated pockets varied among outbreaks. No static spatial partition can efficiently summarize such stochastic, cross-regional phenomena.

A quantitative spatiotemporal analysis, while helpful in identifying shifting patterns in cross-regional disturbance did not reveal a simple way that outbreak patterns could be summarized temporally either. Thus provincial outbreaks are neither wholly regionally synchronized nor wholly temporally punctuated, and there is no single static spatial or temporal partition that can describe more than a fraction of the joint spatiotemporal variability.

6.4.2.2 Municipal grid

At the municipal scale, spatiotemporal analysis showed that outbreaks were sufficiently well-synchronized that spatial partitioning offered little additional benefits in terms of summarizing spatiotemporal variability. The first factor from unrotated S-mode analysis accounted for more than half the variation in aspen ring widths, implying that the mean chronology offered a parsimonious overall summary of municipal outbreak dynamics. On the other hand, T-mode analysis showed that sub-decadal outbreak asynchrony also could account for nearly half of the total spatiotemporal variation. Although the amount of variation accounted for by each view is not additive, these different views are compatible. Indeed, the pattern of sub-decadal outbreak asynchrony provides a meaningful explanation for the prominence of sub-decadal variability in the Cooking L. aspen ring width chronology, shown in chapter three (Fig. 3.8). Thus temporal partitioning (*e.g.* Fig 6.29) offered an effective summary of the data that was complementary to the information portrayed in the mean chronology.

6.4.3 Multi-scale synchrony breakdown on provincial grid

Outbreaks are not globally synchronous, but it is clear that there is some regionalized synchrony. This suggests that global synchrony, typified by FTC outbreak patterns in Ontario, is a useful null model, and that local instances of synchrony breakdown ought to be informative about the nature of local cyclicity and regionalized synchrony.

6.4.3.1 Scaling of outbreak periodicity

Though the municipal periodicity of outbreaks in Alberta is approximately 10 to 12 years, the provincial periodicity of localized outbreaks is closer to 3 years and the local periodicity of province-wide outbreaks is between 16 and 20 years. Indeed, it is possible to identify sub-regional scales in between, where localized outbreaks occur at 5- to 7-year intervals within a municipality. These same periodicities were identified previously in spectral analysis of municipal aspen ring width chronologies (Fig. 3.8), confirming that variation occurring in those frequency ranges is meaningful and can be attributed largely to insect outbreak.

Scaled periodicity is consistent with outbreak patterns reported by Hildahl & Reeks (1960) in Saskatchewan and Manitoba, and helps to explain both their hesitance to employ a single parameter in describing outbreak periodicity and their lack of enthusiasm for the idea of outbreak cycles. Spatial scaling of outbreak periodicity thus appears to be a fundamental and ubiquitous phenomenon that must be considered in any mechanistic hypothesis of forest tent caterpillar outbreaks. Indeed, asynchrony in the sub-decadal range of periodicity may be particularly important, because, upon reviewing the Ontario data, it appears that outbreaks of 1930-1938 in eastern and western Ontario and 1940-1945 in northern Ontario may not be as independent as Sippell (1962) supposed. As with the sub-decadally asynchronous pulses observed in central Alberta, these may arise *via* a process of decadal outbreak-splitting.

The practical implication of scaled outbreak periodicity is that the extent and resolution of sampling are important factors influencing observed patterns. Thus the unbalanced design of the provincial grid was not ideal. Although the extent of sampling at each municipality was roughly similar, the resolution was not, and this could affect observed outbreak periodicity.

That outbreak periodicity is a scaled parameter is, at some level, no surprise because any quasi-synchronous process will exhibit some sort of spatial scaling. The real problem is understanding why outbreak periodicity scales precisely the way it does. Here, the important questions are: (1) where and when does synchrony break down? (2) what global and local mechanisms are responsible? (3) how do these mechanisms conspire to produce compound-cyclic outbreaks with periodicities of 16-20y, 10-12y, 5-7y, and 3-4y at provincial, regional, municipal, and local scales?

6.4.3.2 Regional asynchrony (between municipalities)

The degree of asynchrony between outbreaks in the boreal and parkland regions was most striking. The unrotated T-mode analysis suggested there is a strong tendency for decadal outbreaks to be perfectly out of phase between these regions. On one hand, given that decadal weather patterns are well synchronized across regions (chapter three), it is difficult to imagine how regionalized phase-contrasting could arise from exogenous perturbation; however such patterning could be expected in a self-organized system. On the other hand, regionalized phase-contrasting may have been exaggerated by the orthogonality constraint of unrotated factor analysis. Indeed, under promax rotation, outbreaks appeared to occur as cross-regional anomalies, such that phase-contrasting was neither a persistent nor a particularly boreal/parkland phenomenon.

Cluster analysis suggested that, if anything, it is outbreak periodicity that differs between boreal and parkland regions. This is consistent with the results of stability analysis in chapter five, suggesting there is a weak latitudinal gradient in both stability and periodicity of outbreaks. This interpretation leads to the conjecture that the breakdown in boreal/parkland outbreak synchrony arises from a lack of frequency-locking rather than a lack of phase-locking.

The distinction is a major one. In theory, slow-damping oscillatory populations that are regulated by similar density-dependent structures (and which therefore exhibit similar periodicity in fluctuations) and, yet, fail to phase-lock must be poorly connected *via* dispersal and *via* spatially autocorrelated perturbation. In contrast, oscillatory systems that fail to frequency-lock as a result of having dissimilar intrinsic dynamics are not necessarily poorly connected. Understanding boreal/parkland outbreak asynchrony is therefore largely a matter of understanding regional differences in periodicity. First and foremost is the issue whether regionalization is deterministic or stochastic in origin.

There are many environmental parameters that vary systematically across the boreal/parkland latitudinal gradient, and many of these likely influence tent caterpillar survival. Climate and forest structure, for example, both influence outbreak dynamics in Ontario (Roland *et. al.* 1998, Cooke & Roland 2000), so it seems likely that either could be responsible for regional variation in boreal/parkland outbreak periodicity in Alberta. For instance, the warmer climate of the aspen parkland may lead to high winter survival, thus leading to faster population growth, higher equilibrium densities, and more frequent outbreaks. Such a mechanism has been conjectured to explain the difference in outbreak periodicity between northern and central Ontario (Daniel & Myers 1995). Alternatively, the greater proportion of host trees in the aspen parkland might also lead to more frequent outbreaks, either through reduced food competition or lower dispersal losses. In support of this view, outbreak severity across northcentral Ontario seems to depend partly on the proportion of aspen, although the mechanism is unclear (Roland 1993).

The suite of predators, parasitoids and pathogens associated with forest tent caterpillar appears to be rather similar between boreal and parkland regions (Williams *et. al.* 1996), suggesting that this is not a likely cause of regional differences in outbreak periodicity. At the same time, the effectiveness (and, therefore, relative abundance) of some of these natural enemies could vary geographically in response to spatial gradients in environmental variables such as climate and forest structure. For instance, weather has a strong effect on many processes affecting natural enemy efficiency, such as phenology, feeding, and dispersal, and some species may be better adapted than others to local climatic conditions. Alternatively, as natural enemies are also affected by forest structure, it is possible that higher outbreak frequency in the aspen parkland is a result of natural enemy inefficiencies caused by widespread forest fragmentation associated with agriculture.

That outbreaks occasionally occur in both regions at the same time does not imply temporary bouts of frequency-locking, for two functionally independent oscillating processes differing by only a little in periodicity will appear to fluctuate fairly synchronously when observed over an appropriately chosen narrow time-frame. [The positive correlation between lynx cycles (periodicity = 9.7) and sunspots (periodicity = 11.4) over the periods 1820-1852 and 1879-1905, cited by Royama (1992, his Fig. 6.7), is a famous example of this.] There is therefore no evidence that boreal/parkland synchrony-breakdown is transient.

At the same time, it is difficult to explain how the observed pattern of joint spatiotemporal variability could arise solely from a persistent failure of regionalized population trajectories to lock frequencies. If outbreak periodicity varied smoothly from high to low along a latitudinal gradient, then there should be a striking appearance of latitudinally oriented waves of alternating epidemic and endemic populations that appear to travel northward, and these should break down and reform at regular distance- and frequency-dependent intervals. The complete lack of any such regularity in observed patterns of cross-regional outbreak flow argues against the idea of continuous latitudinal gradients in deterministic outbreak cycles. Latitudinal gradients in periodicity are either not continuous or do not arise through purely deterministic mechanisms.

6.4.3.3 Cross-regional shift

Municipal stand clusters were too isolated from one another to resolve fine-scaled patterns of cross-regional flow. Thus it was not possible to determine whether shifting patterns of outbreak were due to fluid motion or asynchronous outbreak pulses. However, it appeared that there were many modal patterns of outbreak shift, such that outbreaks did not develop according to any obvious systematic pattern. This argues for the importance of stochasticity, although it is not clear how it originates.

6.4.3.4 Local asynchrony (within municipalities)

The rapid decline of outbreak synchrony between pairs of stands separated by less than 50 km implies that some of the breakdown in synchrony occurs within municipalities. Gradients in forest structure seem to contribute little to the rate of decay in distance-dependent synchrony. For example, the rate of distance-dependent synchrony decay at Whitecourt and Drayton Valley was no higher than that observed at Fort McMurray and Conklin, implying that gradients in forest structure across the first two municipalities contributed little to the degree of synchrony breakdown. Data for Dixonville and Cooking L. could not be used to examine this question because the pattern of fragmentation there did not conform to a clear gradient. Data for Peerless L., Athabasca and Frog L. were also unsuitable because there were too few long chronologies to obtain good estimates of distance-dependent synchrony-decay. Because patterns of forest fragmentation were strongly gradient-like at Whitecourt and Drayton Valley, these municipalities could be compared to Fort McMurray and Conklin, where landscapes were continuously forested.

Spatiotemporal factor analysis showed that the pattern of synchrony was affected by gradients in forest structure. Specifically, as indicated by promax-rotated loadings on factors one, three, four, six and nine from T-mode analysis of provincial grid data, outbreaks did not appear to bounce back and forth across continuously forested municipalities such as Fort McMurray or Conklin, but did appear to do so across fragmented municipalities such as Whitecourt and Drayton. This reveals a major limitation in using distance-dependent correlation functions as indicators of spatiotemporal structure, because according to these, the degree of outbreak synchrony was not reduced by large-scale forest fragmentation.

Similar patterns of sub-decadal asynchrony were revealed on the municipal grid. Factor one, in particular, highlighted strong asynchrony between the eastern fragmented landscape and the western continuous forest with regards to localized outbreaks in 1949-1950 and 1957-1960. Due to the limited extent of sampling at Whitecourt and Drayton Valley, one can not judge whether longitudinal asynchrony among forest landscape types there was homologous to sub-decadal outbreak asynchrony on the Cooking L. municipal grid. At the same time, there is no good reason to believe otherwise. On the surface, then, it appears that local forest fragmentation does not consistently lead to earlier, later, or longer local outbreaks, but instead leads to a municipal-scale breakdown in sub-decadal outbreak synchrony.

It is unclear whether sub-municipal, sub-decadal breakdown in outbreak synchrony at Whitecourt, Drayton Valley and Cooking L. is caused by forest fragmentation or some other latitudinally varying parameter, for all three of these municipalities are located on the fringe of the aspen parkland. What is clear is that the mechanism of synchrony breakdown is probably not poor teleconnectivity, for populations separated by less than 50 km are probably well connected *via* dispersal and are probably perturbed by the same suite of climatic fluctuations. The only other possible explanation for outbreak synchrony breakdown is that outbreak cycles are not deterministically driven by a well-behaved predator-prey interaction.

If the natural enemy fauna does not vary over such small distances, this last point further implies that there must be municipal-scale spatial variation either in the efficaciousness of some natural enemies or in the effect of climatic perturbations. The first mechanism would break down the system's deterministic tendency toward synchrony, whereas the second would break down the system's stochastic tendency toward synchrony. Either is possible and there is marginal support for both ideas.

First, fragmentation-caused synchrony breakdown is precisely the sort of mechanism that could explain the "neighbourhood effect" of forest fragmentation on outbreak duration in neighbouring townships (Cooke & Roland 2000). If local forest fragmentation, through its effects on natural enemy behaviour, leads to a larger-scale breakdown in outbreak synchrony, then: (1) outbreaks will tend to appear to last longer at those larger scales, and (2) correlations between forest cover and outbreak duration will increase with increasing spatial scale of analysis - which is precisely the relationship described by Roland (1993) in Ontario. If this is the mechanism for sub-municipal synchrony breakdown in Alberta, then continuously forested landscapes should consistently show higher outbreak synchrony than mixed landscapes. More extensive sampling is required to test this prediction.

If more extensive sampling of continuously forested boreal municipalities revealed outbreak asynchrony comparable to patterns in the aspen parkland, then synchrony breakdown could not be attributed to forest fragmentation. There is actually some hint of this possibility in the available data, for if sub-decadal temporal variability at Whitecourt, Drayton Valley and Cooking L. (Fig. 3.8) is a direct result of sub-decadal, sub-municipal outbreak asynchrony, then similar sub-decadal temporal variability at boreal municipalities (Fig. 3.8) might have a similar cause.

6.4.3.5 Value of increasing extent, resolution, number of municipalities sampled

Although the extent of sampling at each municipality was roughly similar, the resolution was not, and this could affect observed outbreak periodicity. Consequently, the robustness of outbreak patterns reported here should be investigated by increasing the resolution of sampling, especially at Frog. L. and Athabasca. The fact that synchrony begins breaking down at 50 km suggests that the resolution of sampling at all municipalities except Cooking L. was too small. High-resolution, systematic sampling across each municipality might reveal patterns of within-municipality, sub-decadal outbreak asynchrony similar to that revealed at Cooking L. Given the resolution of sampling at Cooking L., was orders of magnitude higher than at other municipalities, a balanced design may be too costly. Randomized, permutational re-sampling may therefore be helpful in obtaining balanced lattices for pattern analysis.

The extent of sampling should be increased at Fort McMurray and Conklin in order to verify that the rate of synchrony decay here is indeed comparable to that at Whitecourt and Drayton Valley; it may well be lower. Similarly, increasing the sampling resolution at Peerless L. and Athabasca to levels used at Fort McMurray and Conklin would provide a better baseline "control" for this comparison.

That synchrony has substantially broken down by 100 km suggests there is plenty of unsampled space on the provincial grid where additional localized asynchronous outbreaks might have occurred. Gaps between Dixonville-Whitecourt and Athabasca-Peerless L. are particularly large and would be worthy of sampling. The discovery of additional localized outbreaks would imply that the periodicity of local outbreaks could be even less than three years.

That outbreak synchrony breaks down at multiple scales suggests it would be highly beneficial to increase the extent and resolution of sampling at each of the municipalities, and to include more municipalities from across the province. Uniform, high-resolution sampling across the province is the only way to clarify whether joint spatiotemporal variability is a result of discrete, asynchronous outbreak pulses or slowly spreading outbreaks.

Now that the baseline chronologies have been developed, additional chronologies could be developed from cores instead of sections. Thus the cost of additional sampling would be much lower than for previous sampling.

6.4.4 Synchrony breakdown on municipal grid

6.4.4.1 Landscape structure and forest fragmentation

Forest cover was not strongly associated with any joint spatiotemporal component of variability. This is a highly informative result because it shows that even though there were large-scale modes of joint spatiotemporal variability, there was no strong, consistent, and persistent tendency for outbreaks in fragmented landscapes to stop or start either earlier or later, or to have higher or lower amplitude, or to have higher or lower periodicity. If there had been any prominent forest structure-based modes of variability such as these, factor analysis would have extracted them - as demonstrated in chapter ten. Thus any such modality must account for a very small fraction of the joint spatiotemporal variability.

6.4.4.1.1 Weak effects of forest structure

Collectively, the unrotated and rotated solutions of both S-mode and T-mode decompositions consistently revealed three modes of variability that related weakly - but with increasing strength - to forest cover measured at small, medium and large scales (Table 6.5). Depending on how the data were decomposed and rotated, these three modes of variability accounted for 10-15% of the total spatiotemporal variation. The first mode ("Ministik fringe gradient" - MFG) emphasized asynchrony between (1) the transitional bands of semi-forested landscape north and east of the continuous forest of Ministik Hills Bird Sanctuary (including some of the Cooking Lake-Blackfoot Grazing Reserve) and (2) the centrally located band of continuous forest, as well as the distally located highly non-forested landscapes. Temporally, the asynchrony was persistent and strongly decadal, with the continuously forested and non-forested phases acting as a diffuse focus for outbreaks in 1950, 1959, 1969, 1979, 1989 and the fringe between them acting as intermediary refugia for localized infestations in 1954, 1963, 1973, 1980, 1986. This mode of variability was also closely associated with the 1986-1994 transitional sequence, which exhibited (1) flow-like patterns within time-slices (*e.g.* 1986-1988: rotational flow from fringe, northeast to southeast; 1990-1994: radial-central implosion into continuous forest at Ministik Hills Bird Sanctuary) and (2) sub-decadally asynchronous outbreak pulses between time-slices (1988 fringe *vs.* 1993 continuous forest + eastern pocket).

The second mode ("eastern two-patch" - E2P) emphasized asynchrony between the mostly continuous forest of Cooking L. Blackfoot Grazing Reserve in the extreme northeast and the largely agricultural area in the extreme southeast. Temporally, the asynchrony was persistent but non-stationary, with strongly periodic sub-decadal asynchrony damping around 1960. This mode of variability was also closely associated with the 1942-1945 transitional sequence, as well as other high-frequency asynchronous behaviour (*e.g.* seemingly eruptive flow in 1986-1988 and 1991-1993 associated with repetitive north-south bouncing motion on east part of grid).

The third mode ("radial three patch" - R3P) emphasized asynchrony between the central core of continuous forest at Ministik Hills Bird Sanctuary and three fragmented patches to the north, southwest, and east. Temporally, asynchrony was persistent but non-stationary, with strongly periodic sub-decadal asynchrony giving way to decadal asynchrony around 1960. This mode of variability was also closely associated with the 1969-1972 transitional sequence. In fact, promax rotation of the S-mode decomposition suggested that the triangular R3P pattern could be viewed as a composition of three separate modes. Most notably, under rotation, the apex of R3P - situated at Hastings Lake - became a separate mode of variability in the form of factor four. Although loadings of factor four (promax, S-mode) do not correlate with forest cover, this highly fragmented area bridges the gap between the continuous forest of Ministik Hills Bird Sanctuary and the highly forested area of Cooking L.-Blackfoot Grazing Reserve.

There is insufficient evidence to conclude resolutely that local forest fragmentation alters local outbreak dynamics. At the same time there is some support for the view that grid-wide outbreaks are comprised of localized outbreak pulse-pairs that are closely situated in time and remotely situated in space and which arise from seemingly eruptive patterns of rapid flow between different types of landscapes. The lack of regularity of these flow patterns and the low association with forest cover suggests this theory is incomplete.

The low correlations are a particular concern for two reasons. First, orthogonality increases the probability of detecting false-positives in non-independent hypothesis tests. Therefore some sort of Bonferroni-like correction or a substantial reduction in the degrees of freedom may be called for in multiple correlation analysis using unrotated factors. Second, with obliquely rotated solutions, the emphasis of simple structure increases the probability of both type I and type II errors, such that small correlations may in fact be significant, while large correlations may be spurious. Thus shared patterns of large-scale spatial structure should first be removed using partial spatial regression so that fine-scale concordance can be tested (Borcard *et. al.* 1992, Legendre 1993, Cooke & Roland 2000).

On the other hand, low correlations between modes of variability and spatial patterns in forest cover might be expected if the effect of fragmentation is pervasive or context-dependent. Consider a landscape such as the municipal grid, with a core patch of continuous forest embedded in a highly fragmented matrix. In a fragmented landscape, the occurrence of an outbreak may be influenced strongly by mass-immigration such that outbreak occurrence is strongly dependent on dynamics in the neighbouring landscape (*i.e.* distance to the nearest core population). This could explain why Hastings Lake, though not particularly fragmented, seems to be a key focal point of outbreak asynchrony on the grid. The high frequency of outbreaks there may be a result of its proximity to populations in the highly continuous forests to the north and south.

If clearings act as barriers to dispersal of both forest tent caterpillars and their natural enemies, then the principal effect of fragmentation may be to merely de-synchronize the system, with no additional effect on local dynamics. In this way, the reduction of dispersal rates effectively serves to stretch space. By stretching space, reduced dispersal could increase the effect of spatial degrees of freedom on the probability of spatiotemporal chaos and self-organization. Prolonged outbreak duration caused by forest fragmentation could be a result of such high-dimensional de-synchronization. This might explain how much of the joint spatiotemporal variability might be caused by forest fragmentation without being associated with spatial patterns of forest cover. Indeed, this could explain how the pervasive phenomenon of sub-decadal, sub-municipal asynchrony arises throughout the aspen parkland.

Alternatively, to the extent fragmentation inhibits parasitoid dispersal more than host dispersal, parasitoid searching efficiency should diminish. If this is the only effect, then host equilibrium densities should rise, outbreak periodicity should increase in frequency, and peak outbreak densities should diminish. The effect on outbreak duration here depends on what is chosen as the outbreak threshold: a low threshold implies outbreak duration increases. Notice here how local dynamics are altered significantly.

6.4.4.1.2 Pervasive instabilities caused by forest fragmentation

If the effect of forest fragmentation is to create predator-free space, then this could enhance any positive density-dependence that might exist in low-density survival (*e.g.* Parry *et. al.* 1997) and thereby increase the opportunity for predation-driven diffusive instabilities. Here there would be no reason to expect local forest fragmentation to have strictly localized effects. Under pervasive local instabilities, synchrony may give way to asynchronous, self-organized behaviour. This suggests that the existence of low-density positive-feedback and the occurrence of predation-driven diffusive instabilities are important hypotheses in need of testing.

In favour of the predation-driven diffusive instability hypothesis is the fact that outbreaks on the municipal grid do appear to exhibit rapid spread from one landscape locale to another. At the same time many outbreaks are terminated before they span the grid. If outbreaks occurred by a global eruptive mechanism, it would be hard to understand, for example, why the 1950 outbreak did not spread west. But if outbreaks are merely fostered by local diffusive instabilities, this could make sense.

6.4.4.1.3 Non-stationarity of fragmentation effects

If forest fragmentation leads to the creation of predation-driven diffusive instabilities, it is unclear why forest-associated modal patterns of asynchrony should evolve over time. On one hand this may be a stochastic, self-organized result of the collective effect of fragmentation-caused de-synchronization. On the other hand, it could signal real changes in local deterministic dynamics caused by real changes in forest cover over time. It is not worthwhile to speculate much beyond this, but the point is worth noting.

6.4.4.2 Self-organization

Departures from perfect outbreak synchrony occurred as a combined result of small differences in phasing, periodicity and amplitude of population cycles on different parts of the grid. Much of this variability was unassociated with static patterns in forest cover, suggesting stochastic self-organization as a possible explanation. Yet classic signs of microscopic spatial patterning (*e.g.* formation of spiral-mosaics) were not observed at this scale, suggesting that joint spatiotemporal variability was largely macroscopic in origin. For instance, the East-West spread of the 1987-88 outbreak across the local grid was not due to microscopic spatial processes; it was part of the regional westbound wave of outbreak that emerged at Frog L. in 1986, passed through the Cooking L. area in 1987-

88, collapsing at Frog L. in 1988, and moved on to Drayton Valley in 1989 while collapsing at Cooking L. If forest tent caterpillar outbreaks on the municipal grid are self-organized or are governed by high-dimensional spatiotemporal chaos, the only evidence is the weak emergence of inter-outbreak refugia.

On the other hand, the tendency for sub-decadal outbreaks to occur on different parts of the grid is very puzzling, and it could be an example of microscopic spatial patterning, as this is a hallmark feature of systems with super-abundant spatial degrees of freedom. Under this hypothesis, however, it would be hard to explain why the negative spatial cross-correlation in outbreak patterns decays rapidly as a function of time, such that non-successive outbreaks are uncorrelated. If this patterning were driven by deterministic high-dimensional spatiotemporal chaos, the patterns should be more persistent.

6.4.4.3 Lagged determinism

Exclusionary patterns of outbreaks could occur if population cycles are partly a result of slowly changing environmental variables that vary spatially. For example: (1) trees heavily defoliated during a first outbreak may have their constitutive defenses activated such that they are less palatable or less nutritional to larvae feeding during a second wave of outbreak (Haukioja 1991a,b); (2) insects that have experienced heavy competition for food may exhibit prolonged effects of nutritional stress through maternal effects (Ginzburg & Taneyhill 1994); (3) populations of insects that have recently become endemic may harbor sub-lethal pathogens or viruses that inhibit reproductive performance (Myers *et. al.* 2000) and persistently retard population growth through vertical transmission (Régnière 1984, Myers 2000). Spatial differences in the action of any of these processes could result simply from environmental and demographic stochasticity.

6.4.4.4 Stochastic perturbation

A reasonable alternative hypothesis is that something tends to split weakly synchronized decadal outbreaks into separate asynchronous events. For example, some agent might temporarily interrupt, in mid-stride, the development of a weakly synchronized grid-wide outbreak; and this interruption might lead to the decline of one component and delayed emergence of its complement. If the agent were stochastic, this might explain why some decadal outbreaks seem to split and some do not. In other words, this might explain why the size of temporal frame in Fig. 6.29 varies as it does. Such a mechanism also might explain why: (1) outbreaks are more frequent in the aspen parkland; (2) population fluctuations exhibit local instability, but not global instability; (3) outbreak dynamics are less locally stable in the aspen parkland; (4) outbreaks are sometimes synchronized across regions. Such a hypothesis could also explain the apparently stochastic nature of localized refugia.

There is some anecdotal evidence that winter temperature could act as a stochastic outbreak-splitting agent. Localized outbreaks in 1938 and 1946 seem to have stalled temporarily, possibly as a result of daily minimum temperatures of -46°C and -43°C occurring on February 8, 1939 and February 1, 1947, respectively. Subsequent outbreaks in 1942 and 1949 seem to be related resurgences that also might have collapsed prematurely as a result of daily minimum temperatures of -44°C and -44°C occurring on January 20, 1943 and January 14, 1950, respectively. In fact, a similar sequence of events might have occurred more recently, for it seems possible that the decline of the large 1987-1988 outbreak in 1989 might have been assisted by the sudden change from Pacific to Arctic weather in early February 1989 in the same way that the collapse of the 1992-1995 outbreak was assisted by a similar change in weather in mid-January 1996 (chapter eight). It is certainly noteworthy that the spatial cross-correlation in impacts between the 1987-1988 and 1992-1995 outbreaks was strongly negative.

Whether the relationship between winter temperatures and outbreak-splitting holds up to formal scrutiny is another question. One problem with a stochastic outbreak-splitting hypothesis is that the sub-decadal splits in decadal outbreaks seem rather more frequent than one would expect by chance alone. A compelling mechanistic explanation might be formulated by considering the non-linear, partially density-dependent perturbation effect of winter temperature on egg survival (chapter eight). A second problem is that climates are colder in the north and, because populations there should be more vulnerable to cold weather anomalies, outbreaks should become increasingly stable as one proceeds from the boreal region to the parkland region. The apparent paradox here may be resolved if it is, instead, the populations in the south that are more vulnerable to cold weather anomalies. It is, for example, entirely possible that winter mortality of tent caterpillars is not determined by the low winter temperature as much as the net change in temperature over a short time (chapter eight). Again though, whether such modifications would help the theory stand up to formal scrutiny is an open question.

Of course it is possible that multiple mechanisms are involved. For example, forest fragmentation may weaken population synchrony such that, in the absence of perturbation, outbreaks appear to flow. Stochastic perturbation then may occasionally disrupt the pattern of smooth flow to create pairs of asynchronous pulses, which, while temporally discrete, are nonetheless functionally associated with one another. Thus both mechanisms may be necessary to account for high-frequency outbreaks and scaled outbreak periodicity.

6.4.5 Asynchronous outbreaks or asynchronous impacts?

It is difficult to imagine a simple mechanism by which successive infestations would occur on different parts of a study area. Yet it is important to do so because such patterns conflict with predictions from simple predator-prey models. Some plausible hypotheses have just been outlined; however none were especially simple.

An alternative explanation may be that it is not the dynamics of the defoliator that are sub-decadally asynchronous, but the impacts of the defoliator. This could occur if, for example, the response of aspen trees to defoliation depends on the occurrence of previous outbreaks.

Consistent with this view is the fact that the negative spatial correlation between successive outbreaks was a result of contrasting spatial patterns in *below-average* growth. In other words, although any given outbreak affected most of the plots, the maximum impact occurred on a subset of those, and it was the location of the *area of maximum* *impact* that tended to shift between sub-decadal outbreaks.

This issue can not be resolved using dendrochronological data because there is no way to distinguish population densities from defoliation impacts. It could be addressed by examining spatial patterns of variation in some measure of defoliation or, better yet, population density.

6.5 Conclusion

The major factor limiting aspen growth in Alberta is defoliation during quasi-periodic outbreaks of the forest tent caterpillar. Forest tent caterpillar outbreaks are not perfectly synchronized at municipal or provincial scales, but they are not random either. They exhibit regional and local coherence over spatial and temporal scales that vary both in time and space. Localized sub-epidemics appear to be a common occurrence, suggesting high-resolution mapping and ground-check sampling is essential in aerial surveys.

Depending on the scale of accounting, outbreak periodicity in Alberta could be said to vary from 3 to 20 years. This corroborates, and even widens the intervals commonly cited in the literature. Thus outbreak periodicity is a scaled quantity that depends how outbreaks are defined in space and time, indicating the importance of scale in studying patterns of forest tent caterpillar outbreaks.

In Alberta, the breakdown of forest tent caterpillar outbreak synchrony occurs in strong association with large-scale gradients in climate and forest structure, and in weak association with small-scale gradients in forest structure and, possibly, the stochastic occurrence of large-scale cold winter weather anomalies. It is not clear whether outbreaks spread *via* a global eruptive mechanism, or whether forest fragmentation leads to local predation-driven diffusive instabilities.

If forest fragmentation in the aspen parkland does not lead to increased outbreak duration, it may be a result of stochastic perturbation. If poorly synchronized, long-lasting outbreaks are often interrupted temporarily by stochastic perturbation, this would explain why outbreaks in the aspen parkland are more frequent and sub-decadally asynchronous. This theory may help to explain why outbreaks in Ontario are more highly synchronized, despite being vulnerable to fragmentation effects and stochastic perturbation by cold weather. First, forest fragmentation may be less extensive (*e.g.* there is no aspen parkland region in Ontario). Second, stochastic perturbation by winter weather anomalies may be less intense, less variable, less periodic, and/or more highly spatially autocorrelated.

Discussions of population synchrony thus far have been excessively oversimplified. Dispersal may act as a synchronizing mechanism, as Barbour (1990) showed; however, it may be a source of de-synchronizing diffusive instability that is only revealed upon habitat fragmentation. Spatially autocorrelated perturbation may act as a synchronizing mechanism, as Moran (1953) showed; however, it may act as a de-synchronizing force if perturbation effects are partially density-dependent. Thus the synchronizing and de-synchronizing effects of dispersal and perturbation may be scaled functions. This argues strongly against the use of simple non-spatial models for representing population interactions. Even explicitly coupled spatially-implicit predator-prey models are insufficient to capture such effects. Fully explicit spatiotemporal representations are essential to obtain the full range of effects of dispersal and perturbation on population synchrony.

Population synchrony, while useful as a concept, is less useful as a hypothesis, because the alternative hypothesis, namely asynchrony, can take many forms from randomness to scaled clustering. Refuting the population synchrony hypothesis therefore leads inevitably to the analysis of specific patterns of spatiotemporal decoherence and a discussion of the mechanisms of synchrony and synchrony breakdown. More sophisticated spatiotemporal models are required to generate more refutation-worthy hypotheses. This argues strongly against the use of general theoretical models and for system-specific process-oriented models.

6.6 Literature Cited

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Table 6.1. Shifting disturbances across the provincial grid 1936-1994, revealed by promax-rotated T-mode decomposition. Loading differences computed as the vertical change in factor loading for pulses highlighted in Fig. 6.13. Spatial modes of shift in Fig. 6.14.

pulse	factor	temporal loading difference	pulse disturbance geometry					associated local/minor disturbance	
			start year	end year	interval	closest major disturbance	proximity to major	year	municipality [location]
1	8	-1.00	1940	1943	3	1942	0	1940	Athabasca
2	8	1.04	1943	1945	2	1942	1	1946	Dixonville[N]
3	4	-1.36	1946	1951	5	1949	0	1946	Peerless, Frog L.[S]
4	5	0.89	1948	1952	4	1949	0	1951	Athabasca, Whitecourt[W]
5	2	-1.11	1953	1956	3	1957	1	1953	FtMcMurray[N], Conklin[S]
6	4	1.50	1951	1955	4	1957	2	1955	Drayton
7	3	-0.89	1960	1962	2	1962	0	1960	Whitecourt[E], Drayton[W]
8	6	1.07	1960	1963	3	1962	0	1960	Whitecourt[E], Drayton[W]
9	6	-1.03	1963	1965	2	1962	1	1965	Dixonville[N]
10	2	-1.20	1965	1968	3	1968	0	1965	Dixonville[N]
11	7	1.44	1974	1978	4	1978	0	1973	Conklin
12	3	-0.92	1978	1980	2	1978	0	1980	Drayton[E], Whitecourt[W]
13	1	1.52	1983	1987	4	1987	0	1982	entire northwest boreal
14	5	1.02	1986	1988	2	1987	0	1989	Drayton[W], Whitecourt[W]
15	9	-1.36	1990	1994	4	1994	0	1990	Frog L.

Table 6.2. Environmental correlations for factors derived from unrotated and promax-rotated S-mode decomposition of Cooking. L. municipal grid data 1929-1995. Table shows correlations between: (1) spatial factor loadings and altitude; (2) spatial factor loadings and forest cover measured at various spatial scales; (3) temporal factor scores and precipitation. Scale of forest cover measurement refers to distance along one side of a square centered on each of 66 stands. Precipitation is from instrumental records from Edmonton International Airport 1929-1995. Correlations greater than 0.25 or less than -0.25 shown in bold.

rotat.	fact.	alt.	forest cover						precip.
			53m	106m	212m	425m	850m	1700m	
none	1	-0.18	-0.05	0.11	0.13	0.09	0.11	0.06	**0.45**
	2	-0.19	0.17	**0.29**	0.17	-0.03	0.00	-0.01	-0.11
	3	**0.33**	0.04	0.09	0.09	-0.09	0.04	0.12	0.17
	4	0.05	0.21	0.14	0.14	**0.26**	0.24	0.11	-0.04
	5	-0.07	-0.08	-0.08	-0.19	-0.07	-0.06	-0.01	0.24
	6	-0.18	-0.05	-0.15	-0.24	-0.21	-0.30	**-0.38**	-0.11
	7	0.06	0.20	0.05	0.04	0.07	0.13	0.20	0.00
	8	0.25	-0.04	-0.09	-0.09	0.01	0.08	0.09	0.15
	9	0.13	0.05	-0.10	-0.03	0.07	-0.06	0.00	-0.09
promax	1	0.00	0.19	0.22	0.18	0.03	0.04	-0.06	**0.31**
	2	**0.37**	-0.14	-0.06	0.03	-0.04	0.08	0.21	**0.48**
	3	-0.16	-0.10	-0.18	-0.09	0.01	-0.07	-0.12	0.24
	4	0.02	0.01	-0.10	-0.09	0.18	0.11	0.07	**0.35**
	5	-0.18	0.01	0.19	0.17	0.05	0.08	0.09	0.20
	6	-0.21	-0.13	-0.11	-0.20	**-0.27**	**-0.32**	-0.24	**0.28**
	7	-0.06	0.08	0.11	0.00	0.02	0.16	0.17	**0.34**
	8	0.02	-0.15	-0.07	-0.04	0.03	0.06	0.02	0.06
	9	-0.01	0.20	0.24	**0.31**	0.21	**0.26**	**0.30**	-0.03

Table 6.3. Environmental correlations for factors derived from unrotated and promax-rotated T-mode decomposition of Cooking. L. municipal grid data 1930-1995. Table shows correlations between: (1) spatial factor scores and altitude; (2) spatial factor scores and forest cover measured at various spatial scales; (3) temporal factor loadings and precipitation. Scale of forest cover measurement refers to distance along one side of a square centered on each of 67 stands. Precipitation is from instrumental records from Edmonton International Airport 1930-1995. Correlations greater than 0.25 or less than -0.25 shown in bold.

rotat.	fact.	alt.	forest cover						precip
			53m	106m	212m	425m	850m	1700m	
none	1	-0.21	-0.08	0.00	-0.07	-0.13	-0.18	-0.15	-0.22
	2	0.23	-0.07	-0.19	-0.23	-0.17	-0.15	-0.02	0.10
	3	-0.04	0.13	0.10	0.04	-0.20	-0.22	-0.25	-0.21
	4	-0.03	0.00	-0.18	-0.03	0.15	-0.01	-0.03	-0.16
	5	0.04	-0.25	-0.17	-0.15	-0.17	-0.23	**-0.26**	0.06
	6	0.21	0.14	0.25	**0.31**	0.17	**0.27**	**0.30**	0.00
	7	-0.22	0.08	0.04	0.01	0.02	-0.01	-0.05	**-0.29**
	8	0.10	-0.08	-0.07	-0.02	-0.14	-0.03	0.00	0.06
	9	-0.17	0.10	0.17	0.14	0.05	0.17	0.23	-0.10
promax	1	-0.16	-0.12	-0.07	-0.10	-0.07	-0.16	-0.16	-0.21
	2	**-0.26**	-0.13	-0.07	-0.15	-0.18	-0.18	-0.19	0.01
	3	-0.09	0.12	-0.05	-0.05	0.02	0.00	0.08	-0.18
	4	0.05	0.06	0.25	0.13	-0.16	-0.01	0.05	-0.03
	5	**-0.28**	0.14	**0.27**	**0.26**	0.20	**0.26**	0.23	-0.21
	6	-0.17	0.06	-0.01	-0.05	-0.17	**-0.27**	**-0.34**	**-0.30**
	7	0.18	-0.17	-0.12	-0.19	-0.17	-0.10	0.02	0.11
	8	0.23	-0.07	-0.07	0.07	0.07	0.04	0.06	-0.02
	9	0.16	-0.04	-0.03	0.03	-0.08	0.01	0.03	-0.04

Table 6.4. Spatiotemporal exclusion between pairs of disturbance pulses on the Cooking L. municipal grid 1929-1995, as revealed by promax-rotated T-mode decomposition. Loading differences, shown as highlighted portions of factor loading plots in Fig. 6.28, are computed as the difference in loading on a given factor between two years marking the occurrence of successive disturbances. Large differences in factor loadings over long intervals indicate disturbance asynchrony. The spatial modes of exclusion are reflected in factor scores, mapped in Fig. 6.29. The mean interval between exclusionary disturbances is 6.0 years. According to this decomposition, fourteen discrete outbreak disturbances of varying size and intensity are revealed in close conjunction with the years 1930, 1937, 1942, 1946, 1950, 1954, 1957, 1964, 1968, 1972, 1976, 1982, 1987, 1994, yielding a grid-wide local outbreak periodicity of 4.8 years.

disturbance pair no.	year of disturbance pulse: initial	year of disturbance pulse: successor	disturbance interval	factor number	loading difference
1	1930	1936	6	2	-0.74
2	1938	1941	3	9	1.41
3	1944	1949	5	7	0.89
4	1945	1954	9	5	1.07
5	1951	1957	6	1	-1.61
6	1959	1964	5	8	0.78
7	1964	1972	8	3	0.74
8	1976	1983	7	3	1.17
9	1981	1987	6	6	0.52
10	1988	1993	5	4	-1.31

Table 6.5. Three patterns of spatiotemporal variability identified by rotated factor analysis that are associated with spatial patterns in forest cover across Cooking L. municipal grid. Interpretations provided in main text.

modal pattern[1]	anal. mode[2]	rotation	factor no.[3]	λ[4]	r[5]	scale[6] (m)	scores (Fig.)	loadings (Fig.)
MFG	S	none	2	0.040	0.28	106	6.15	6.16
		promax	5	0.055	0.19	106	6.20	6.21
	T	none	(4)	0.048	(-0.18)	106	6.24	6.23
		promax	4	0.051	0.25	106	6.28	6.27
E2P	S	none	4	0.033	0.26	425	6.15	6.16
		promax	9	0.022	0.31	212	6.20	6.21
	T	none	6	0.039	0.31	212	6.24	6.23
		promax	5	0.051	0.27	106	6.28	6.27
R3P	S	none	6	0.021	-0.38	1700	6.15	6.16
		promax	6	0.052	-0.32	850	6.20	6.21
	T	none	5	0.044	-0.26	1700	6.24	6.23
		promax	6	0.047	-0.34	1700	6.28	6.27

[1] MFG: Ministik fringe gradient; E2P: eastern two-patch; R3P: radial three-patch.

[2] Decompositional mode of factor analysis (S: spatial, T: temporal).

[3] Parentheses on unrotated T-mode factor four indicate a negative correspondence with rotated T-mode factor four. This negative correspondence, which is an arbitrary consequence of decomposition, explains why the correlation with forest structure is opposite in sign to that for rotated T-mode factor four. This is why parentheses have been placed around that *r* value as well.

[4] Proportion of variation accounted for by factor.

[5] Maximum correlation between spatial loadings/scores and forest cover.

[6] Scale of forest cover measurement that maximized *r*.

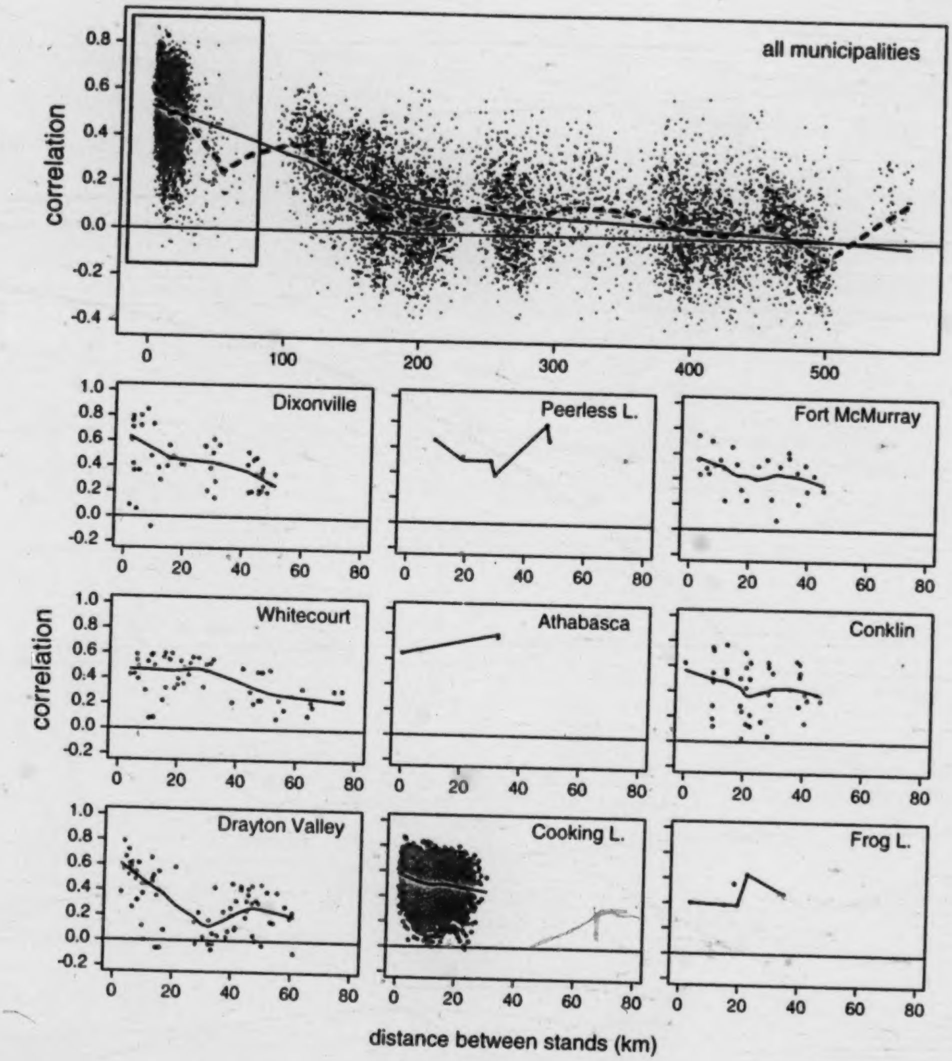

Figure 6.1. Distance-dependent synchrony decay among pairs of stand-wise aspen ring width chronologies 1936-1994. Top panel shows pattern of decay across entire province. Bottom panels shows decay within each municipality. Curves fit by lowess regression with smoothing parameter f = 0.5. Flexible curve in top panel (dashed) fit using f = 0.1.

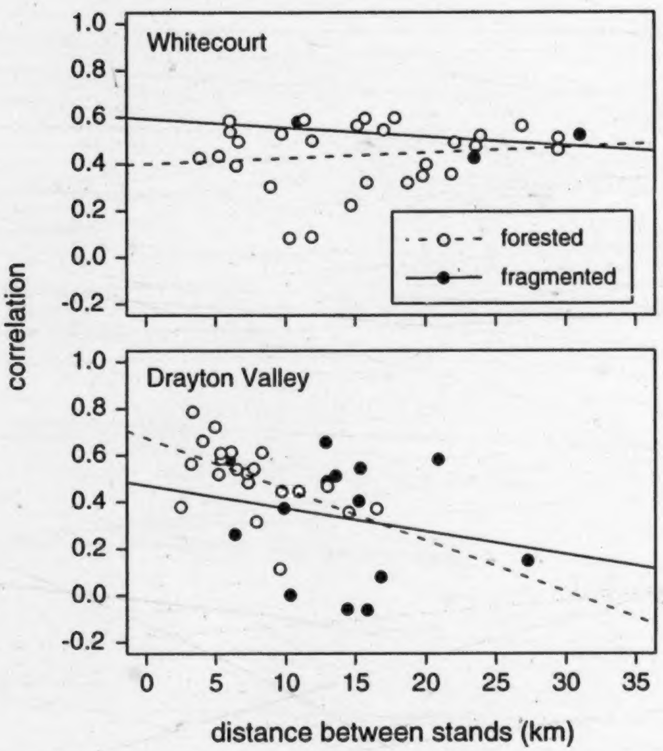

Figure 6.2. Distance-dependent synchrony decay among pairs of stand-wise aspen ring width chronologies within landscape clusters at two municipalities. Regression lines show no difference in the pattern of decay among landscape types.

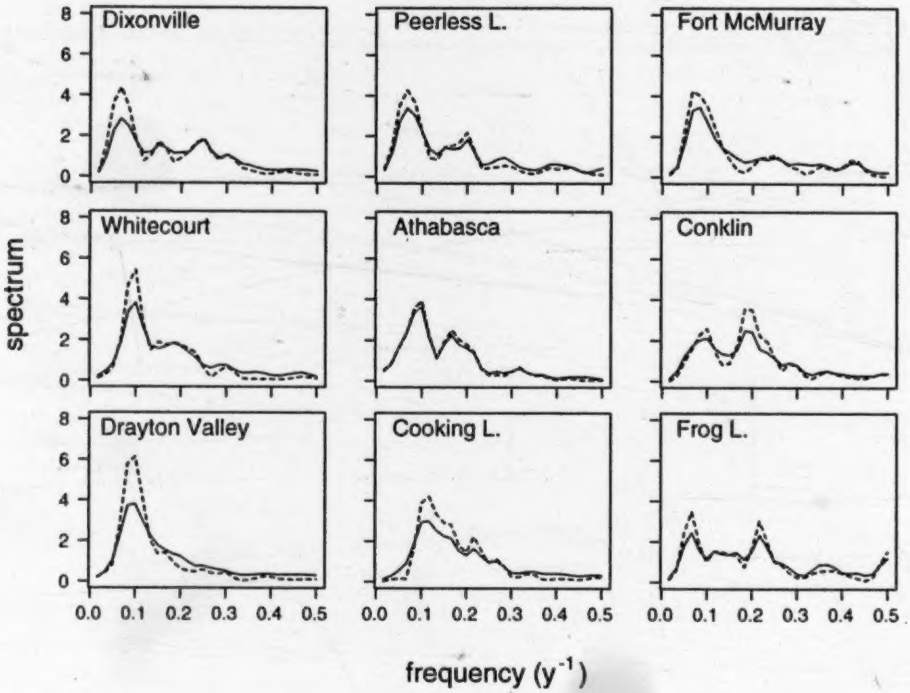

Figure 6.3. Comparison, for each municipality, between the spectrum of the mean municipal aspen ring width chronology (-----) and the mean of all stand-wise spectra (——).

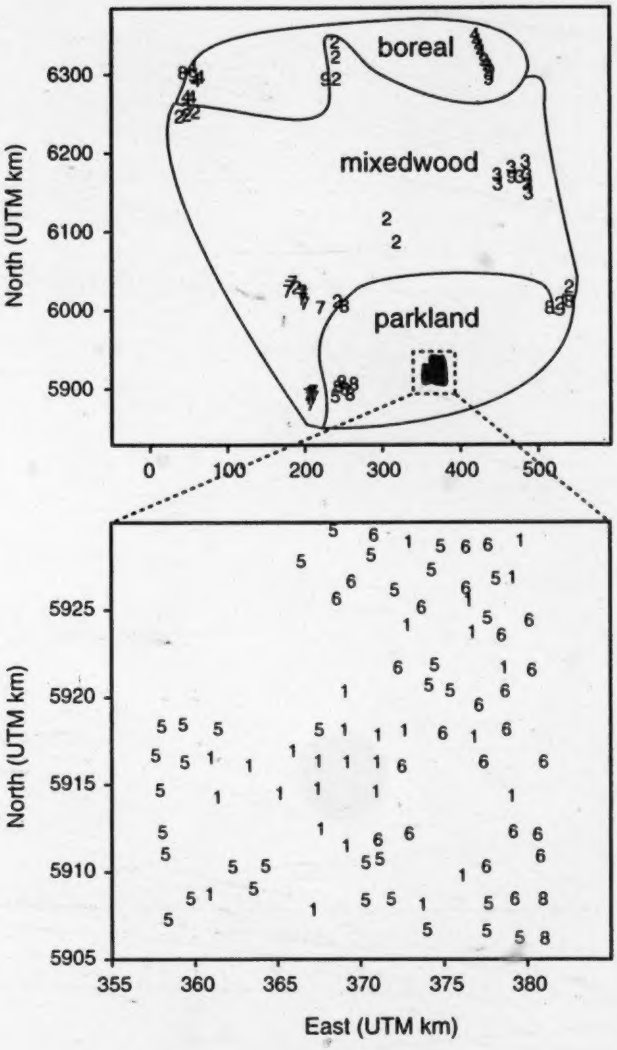
boreal
mixedwood
parkland
North (UTM km)
6300
6200
6100
6000
5900
0
100
200
300
400
500
North (UTM km)
5925
5920
5915
5910
5905
355
360
365
370
375
380
East (UTM km)

Figure 6.4. Results from stand-level *k*-means cluster analysis (k=9) mapped in geographic space. Bottom panel shows close-up view of Cooking L. municipal grid. Numerical symbols indicate stand-level cluster assignment. Clustering with k=3 suggests the nine clusters can be aggregated into three larger regions, as shown.

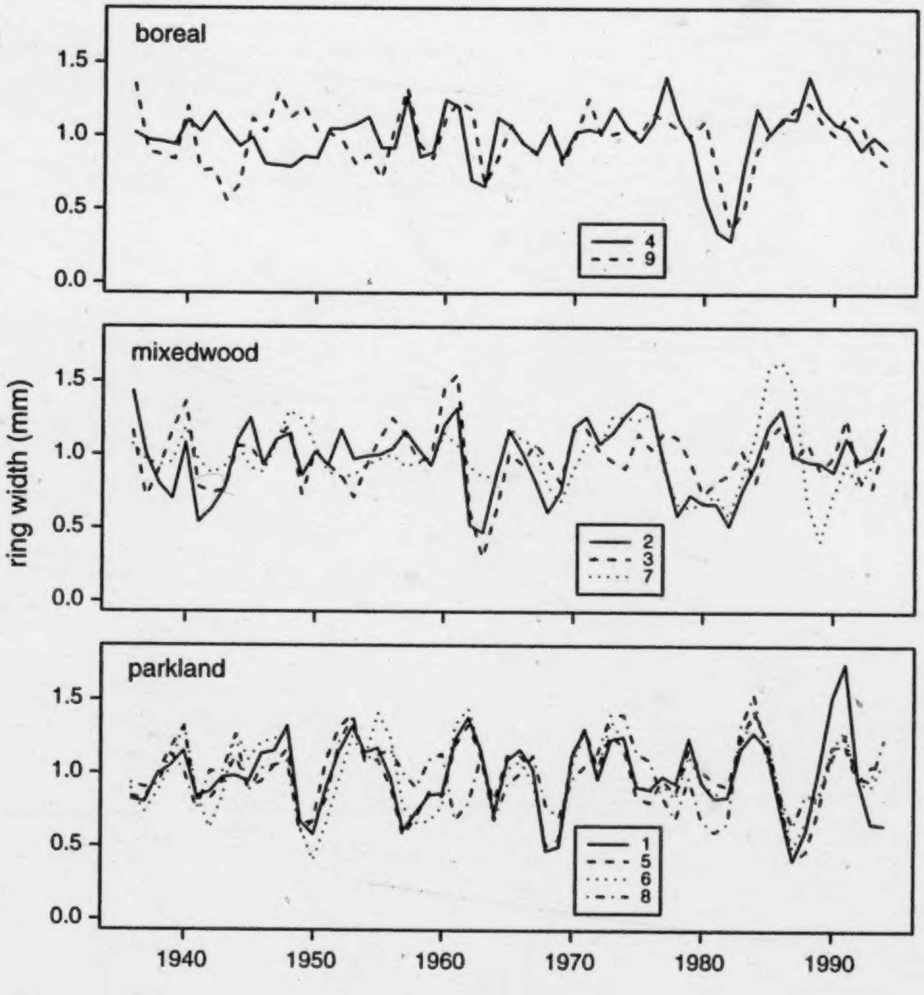

Figure 6.5. Mean chronologies for each of nine clusters derived from *k*-means cluster analysis, aggregated into three geographic regions of similarity. Legends show cluster number. Individual stands mapped in Fig. 6.4 according to cluster assignment.

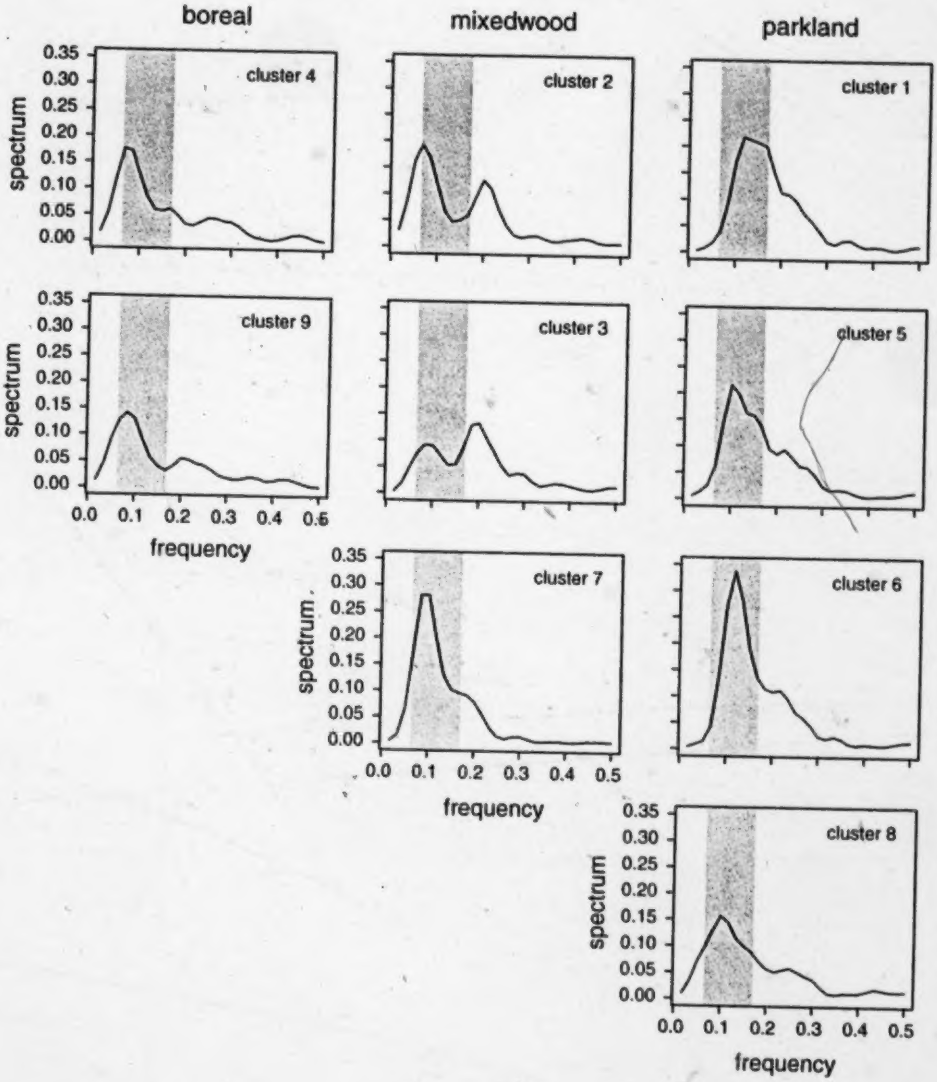

Figure 6.6. Spectra of cluster-wise aspen ring width chronologies of Fig. 6.5, arranged in columns, left to right, by latitudinal region. Shaded region indicates 6 to 16-year range of periodicity. Note lower frequency of disturbance in boreal region, higher in parkland.

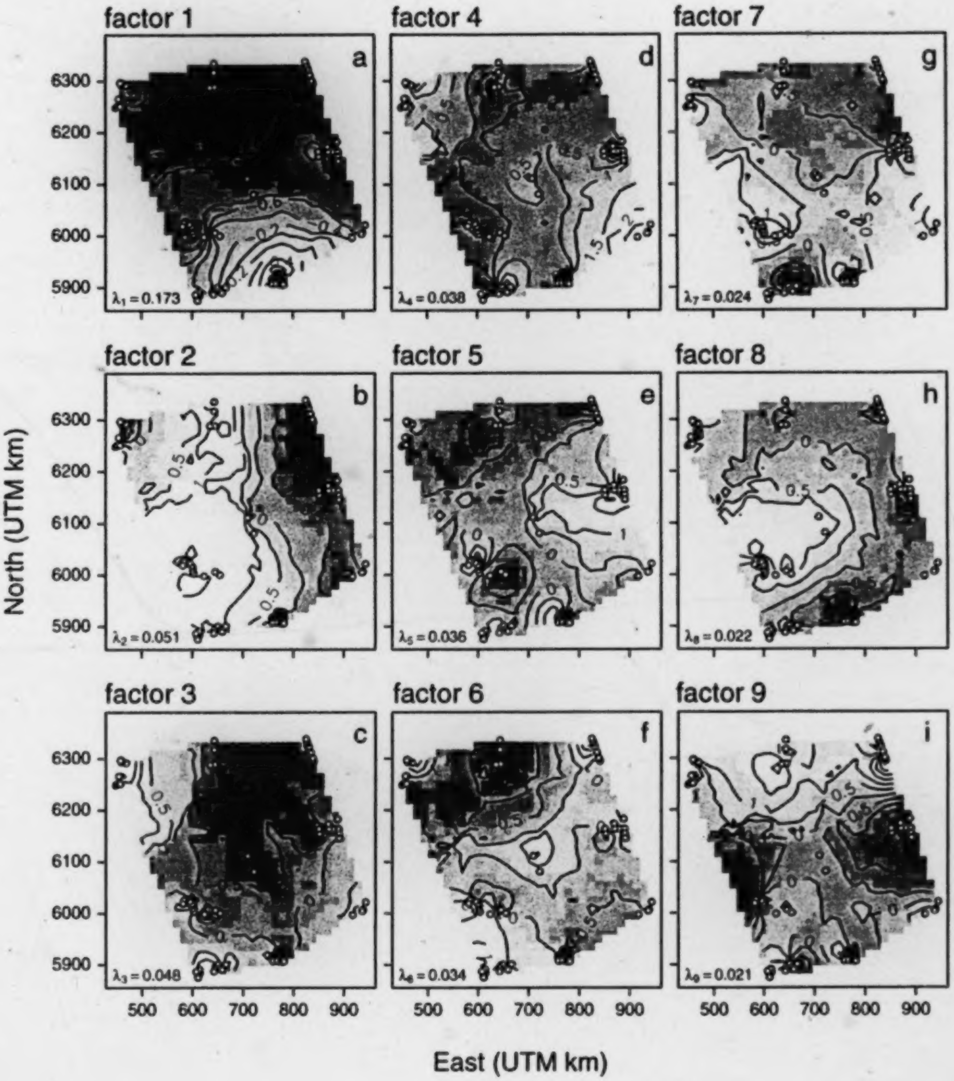
factor 1
factor 4
factor 7
factor 2
factor 5
factor 8
factor 3
factor 6
factor 9
a
b
c
d
e
f
g
h
i
$\lambda_1 = 0.173$
$\lambda_2 = 0.051$
$\lambda_3 = 0.048$
$\lambda_4 = 0.038$
$\lambda_5 = 0.036$
$\lambda_6 = 0.034$
$\lambda_7 = 0.024$
$\lambda_8 = 0.022$
$\lambda_9 = 0.021$
North (UTM km)
6300
6200
6100
6000
5900
500
600
700
800
900
East (UTM km)

Figure 6.7. Scores for first nine unrotated factors from T-mode analysis of provincial grid data.

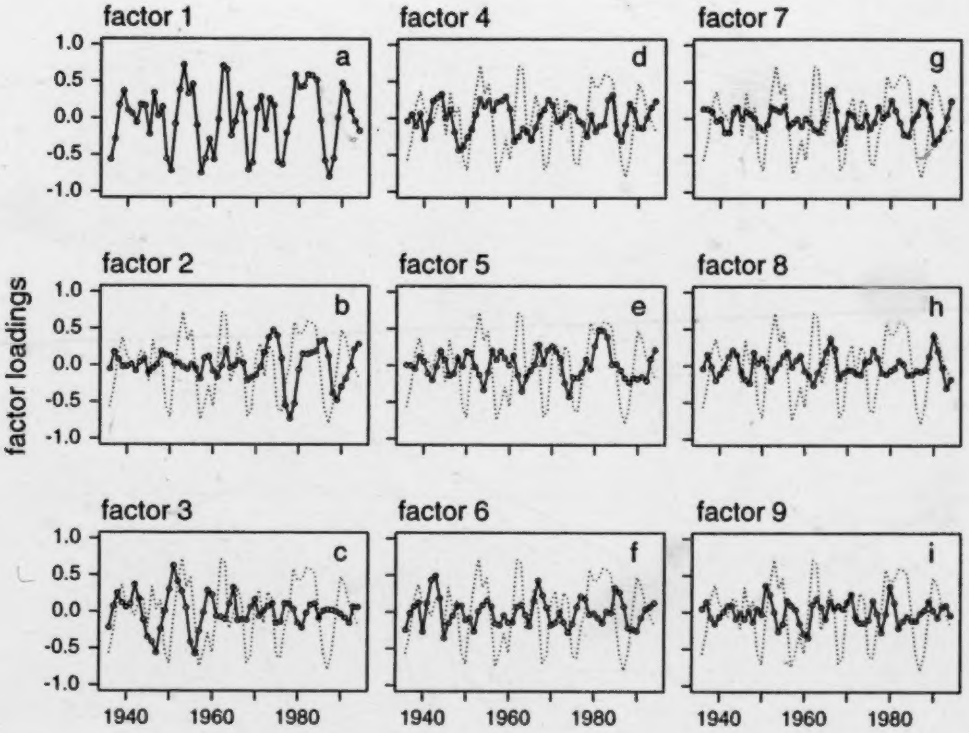

Figure 6.8. Loadings for first nine unrotated factors from T-mode analysis of provincial data. Dotted line indicates loadings for factor 1.

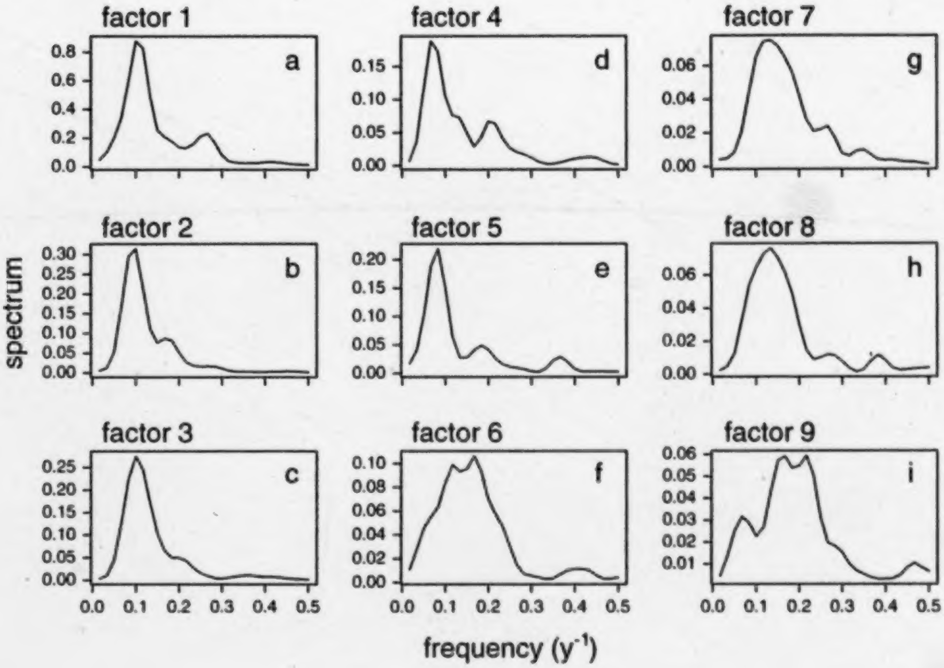

Figure 6.9. Spectra of loadings in Fig. 6.8.

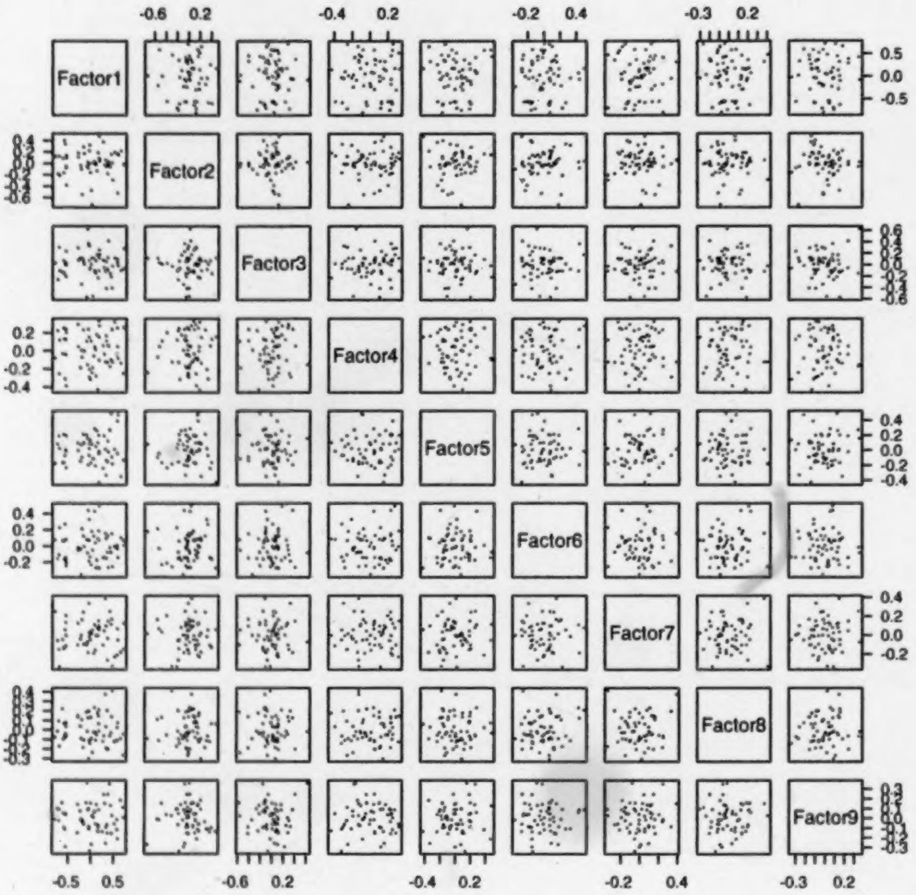

Figure 6.10. Pairwise plots of unrotated loadings in Fig. 6.8.

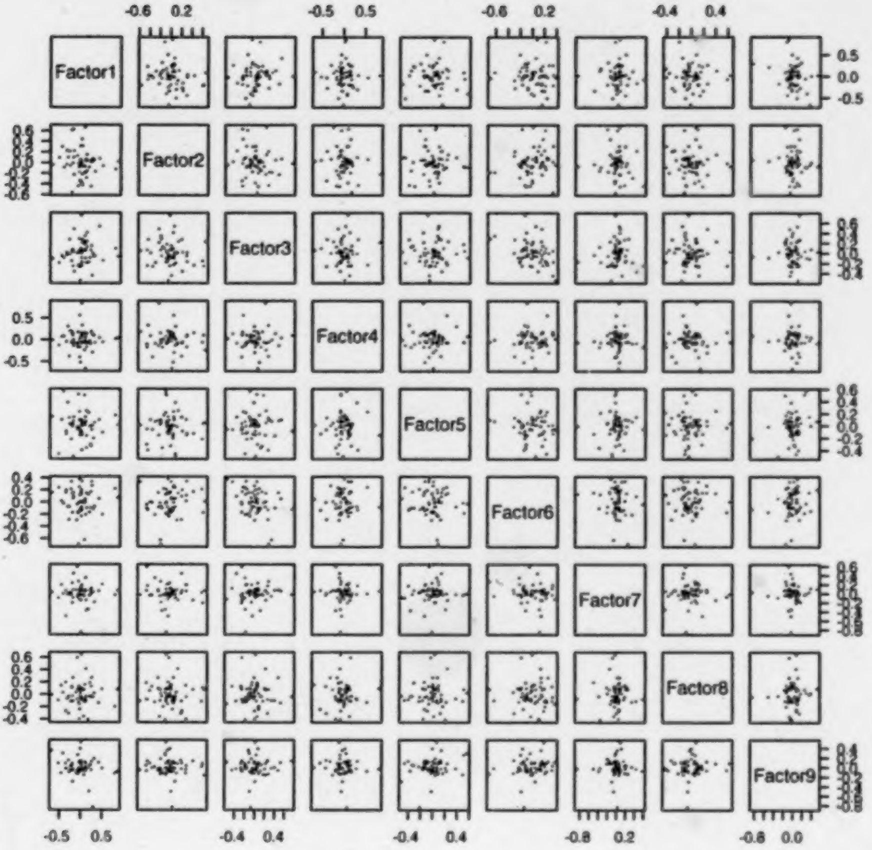

Figure 6.11. Pairwise plots of promax-rotated loadings in Fig. 6.12.

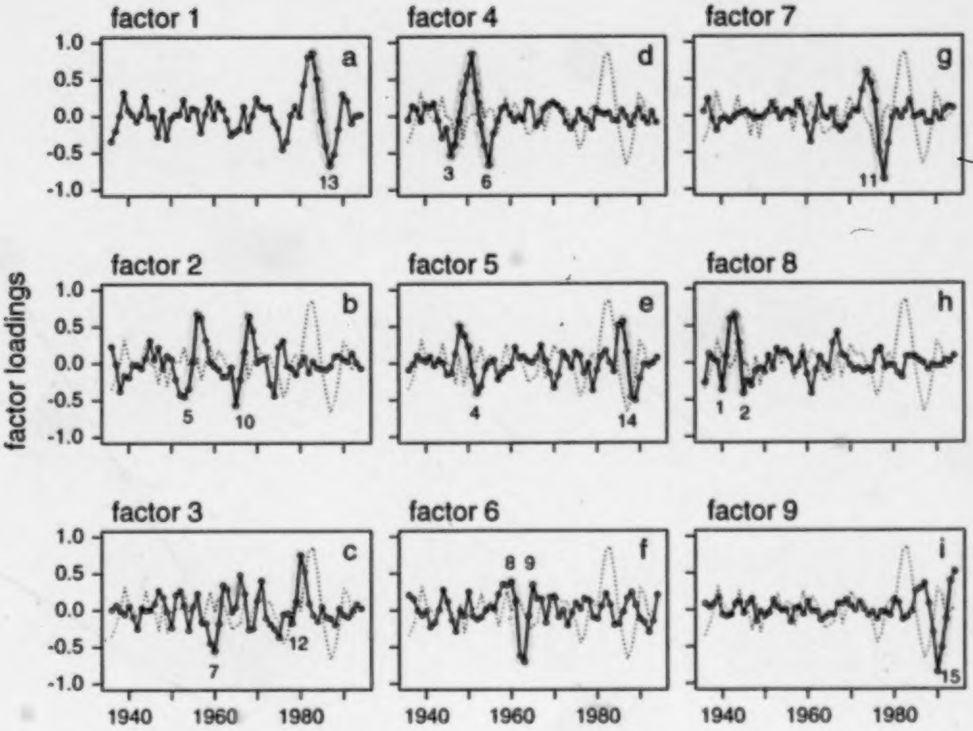

Figure 6.12. Loadings for first nine promax-rotated factors from T-mode analysis of provincial data. Highlighted segments (numbered from 1 to 15, as in Table 6.1) indicate disturbance pulses that tend to spread according to the patterns shown in corresponding scores (mapped in Fig. 6.13). Dotted line indicates factor 1 loadings.

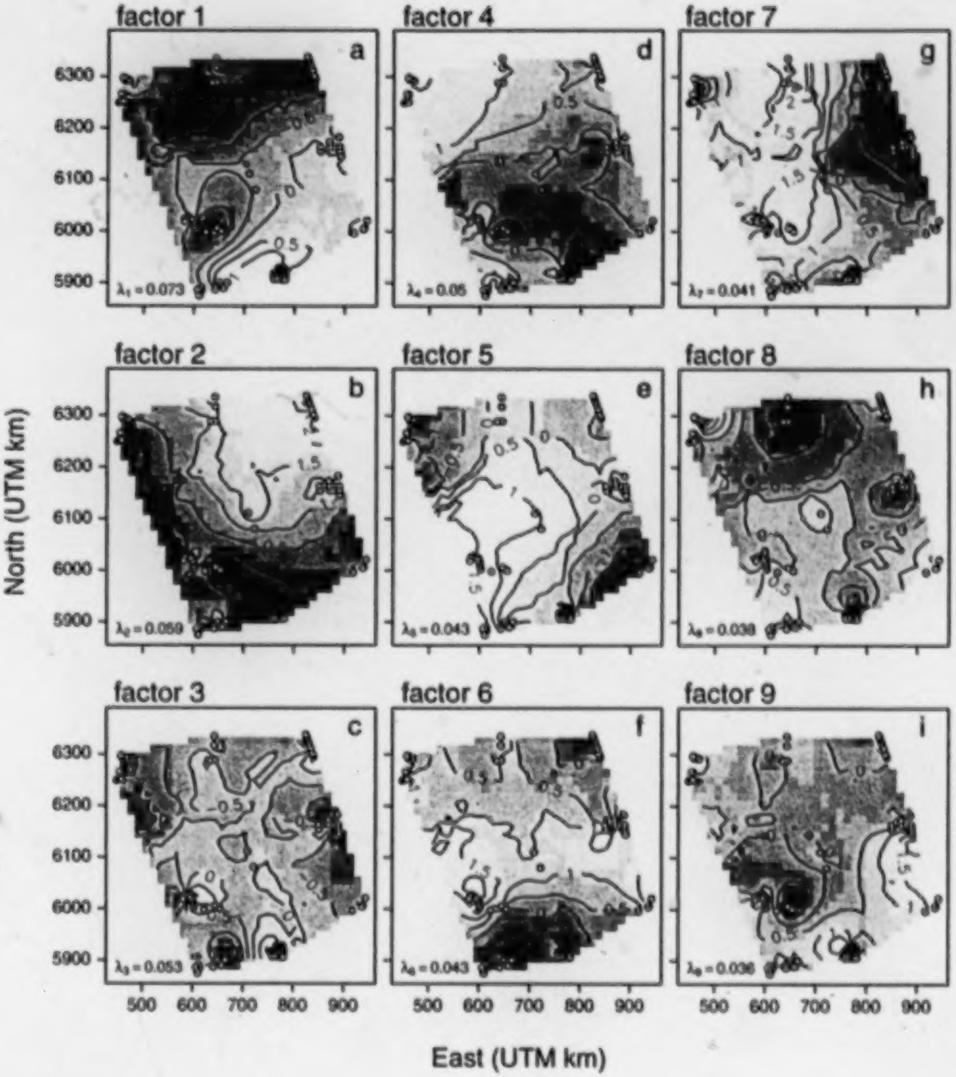
factor 1
a
factor 4
d
factor 7
g
factor 2
b
factor 5
e
factor 8
h
factor 3
c
factor 6
f
factor 9
i
North (UTM km)
6300
6200
6100
6000
5900
$\lambda_1 = 0.073$
$\lambda_4 = 0.05$
$\lambda_7 = 0.041$
$\lambda_2 = 0.059$
$\lambda_5 = 0.043$
$\lambda_8 = 0.038$
$\lambda_3 = 0.053$
$\lambda_6 = 0.043$
$\lambda_9 = 0.036$
500
600
700
800
900
East (UTM km)

Figure 6.13. Scores for first nine promax-rotated factors from T-mode analysis of provincial grid data.

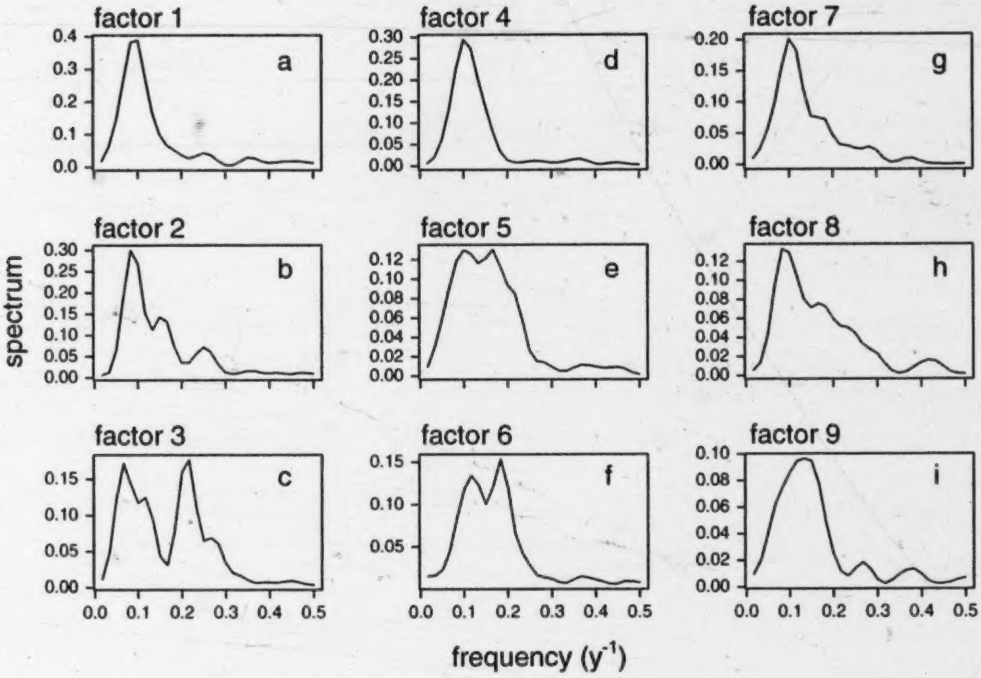

Figure 6.14. Spectra of loadings in Fig. 6.12.

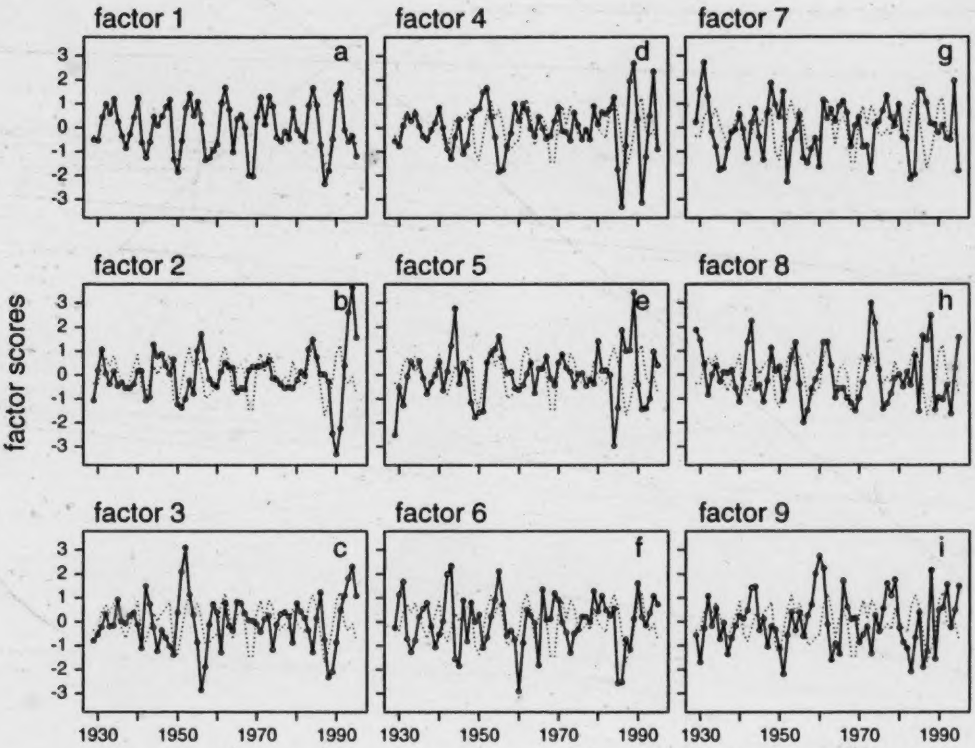

Figure 6.15. Temporal scores from unrotated S-mode spatiotemporal factor analysis of aspen ring width chronologies from the Cooking L. municipal grid. Dotted line indicates scores for factor 1.

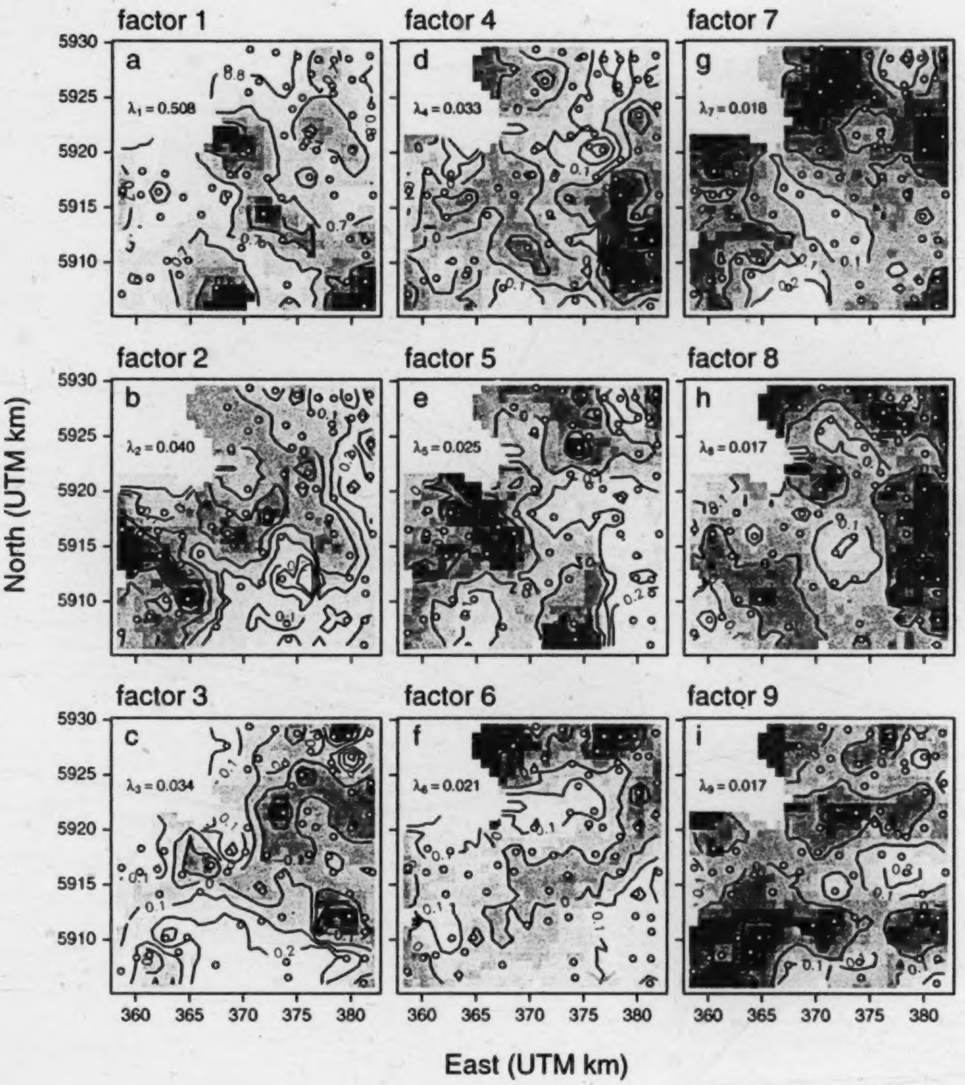
factor 1
a
$\lambda_1 = 0.508$
factor 4
d
$\lambda_4 = 0.033$
factor 7
g
$\lambda_7 = 0.018$
factor 2
b
$\lambda_2 = 0.040$
factor 5
e
$\lambda_5 = 0.025$
factor 8
h
$\lambda_8 = 0.017$
factor 3
c
$\lambda_3 = 0.034$
factor 6
f
$\lambda_6 = 0.021$
factor 9
i
$\lambda_9 = 0.017$
5930
5925
5920
5915
5910
North (UTM km)
360
365
370
375
380
East (UTM km)

Figure 6.16. Spatial loadings from unrotated S-mode spatiotemporal factor analysis of aspen ring width chronologies from the Cooking L. municipal grid.

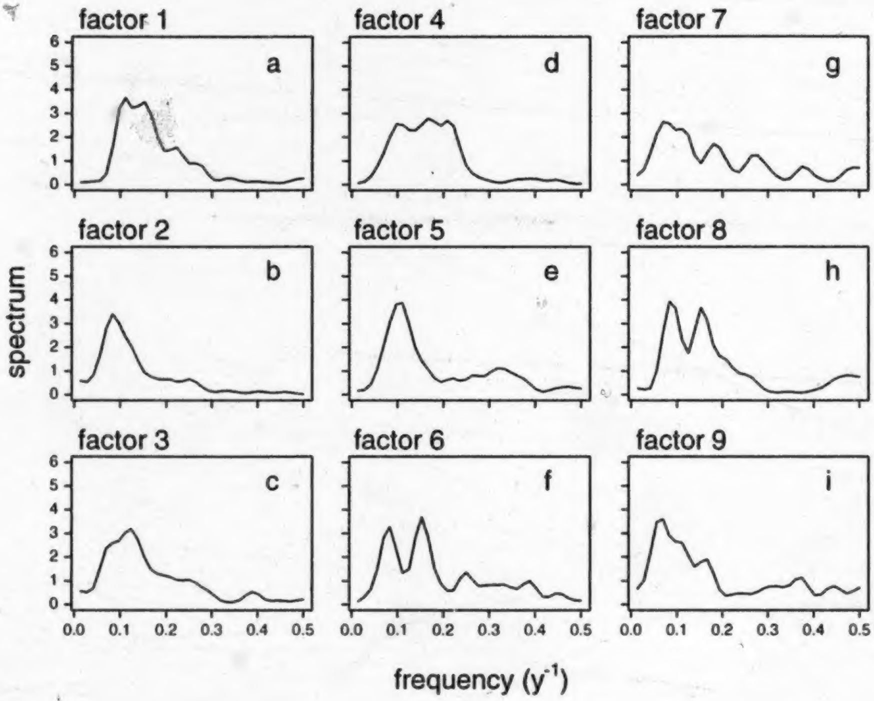

Figure 6.17. Spectra of temporal scores from unrotated S-mode factor analysis of aspen ring width chronologies from the Cooking L. municipal grid, shown in Fig. 6.15.

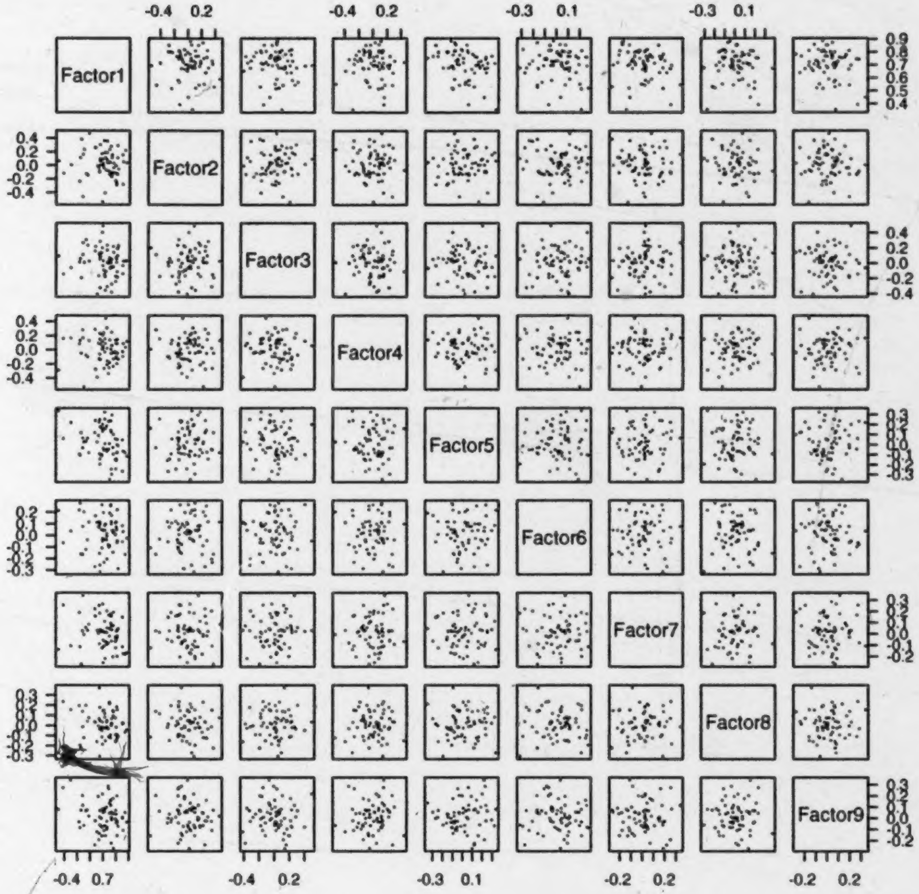

Figure 6.18. Pairwise plots of unrotated loadings in Fig. 6.16.

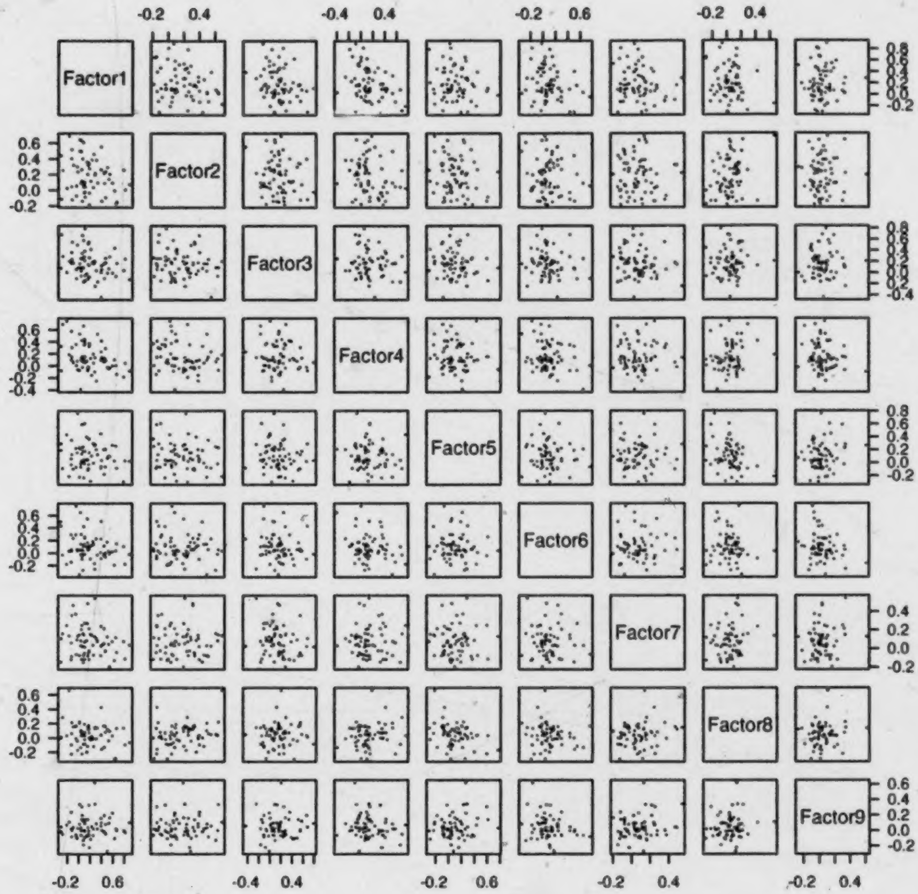

Figure 6.19. Pairwise plots of rotated loadings in Fig. 6.21.

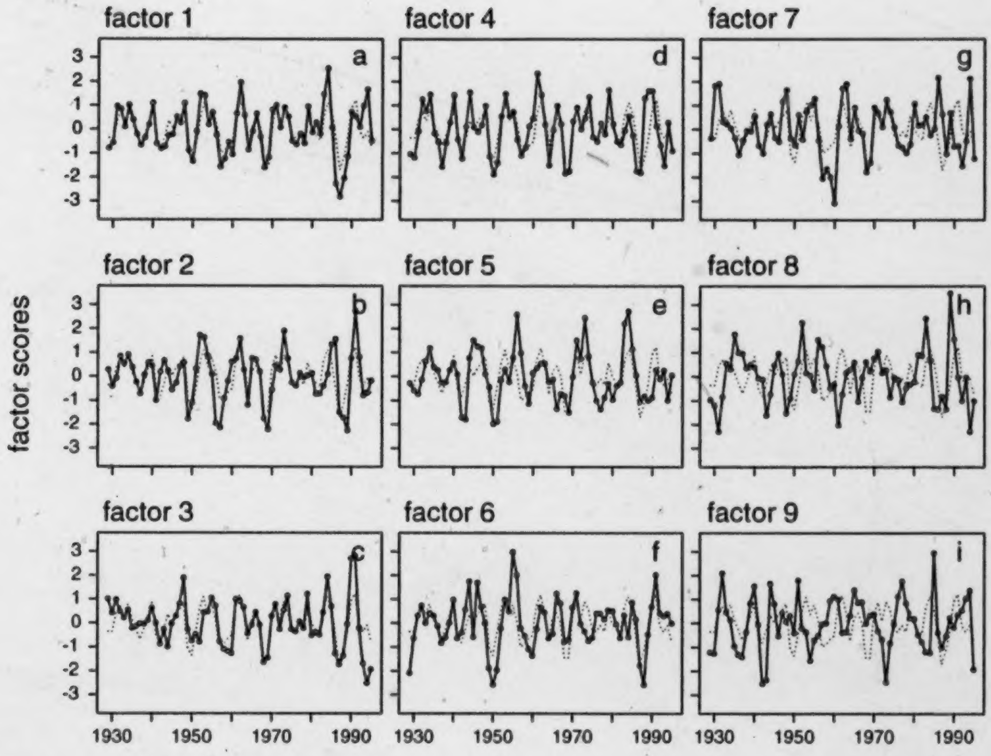

Figure 6.20. Temporal scores from promax-rotated S-mode spatiotemporal factor analysis of aspen ring width chronologies from the Cooking L. municipal grid. Dotted lines indicate factor 1 scores from unrotated S-mode analysis in Fig. 6.15.

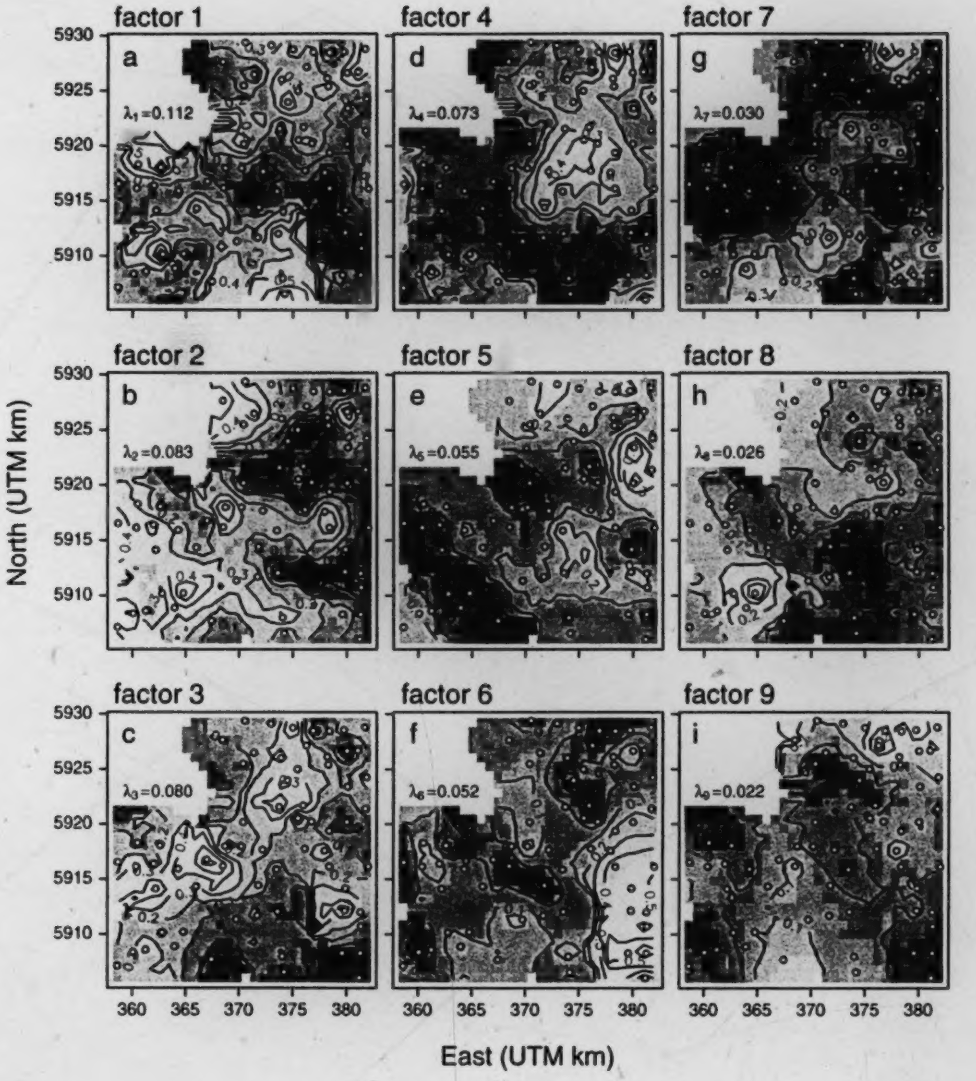
factor 1
a
λ1=0.112
factor 4
d
λ4=0.073
factor 7
g
λ7=0.030
factor 2
b
λ2=0.083
factor 5
e
λ5=0.055
factor 8
h
λ8=0.026
factor 3
c
λ3=0.080
factor 6
f
λ6=0.052
factor 9
i
λ9=0.022
5930
5925
5920
5915
5910
North (UTM km)
360
365
370
375
380
East (UTM km)

Figure 6.21. Spatial loadings from promax-rotated S-mode spatiotemporal factor analysis of aspen ring width chronologies from the Cooking L. municipal grid.

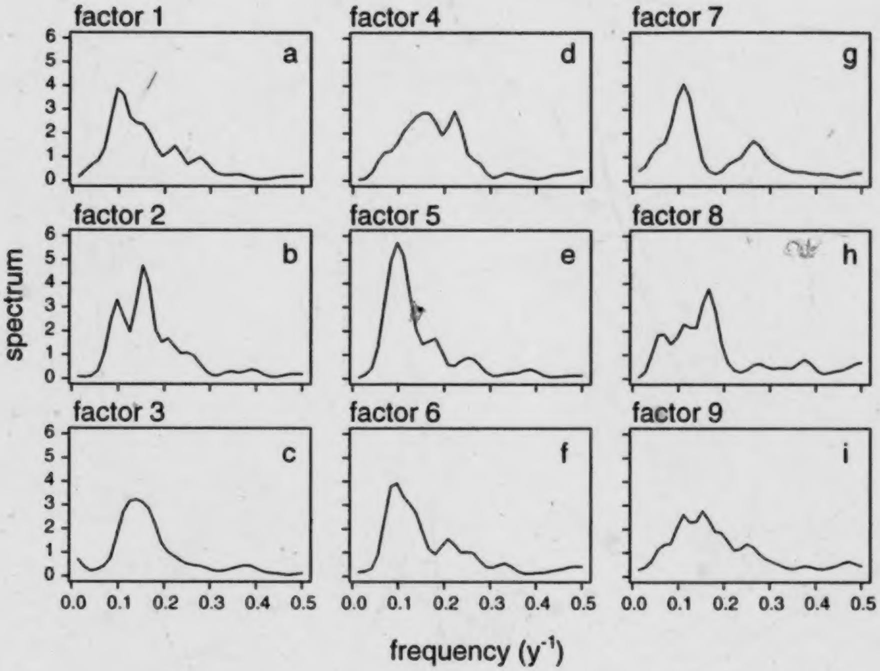

Figure 6.22. Spectra of temporal scores from promax-rotated S-mode factor analysis of aspen ring width chronologies from the Cooking L. municipal grid, shown in Fig. 6.20.

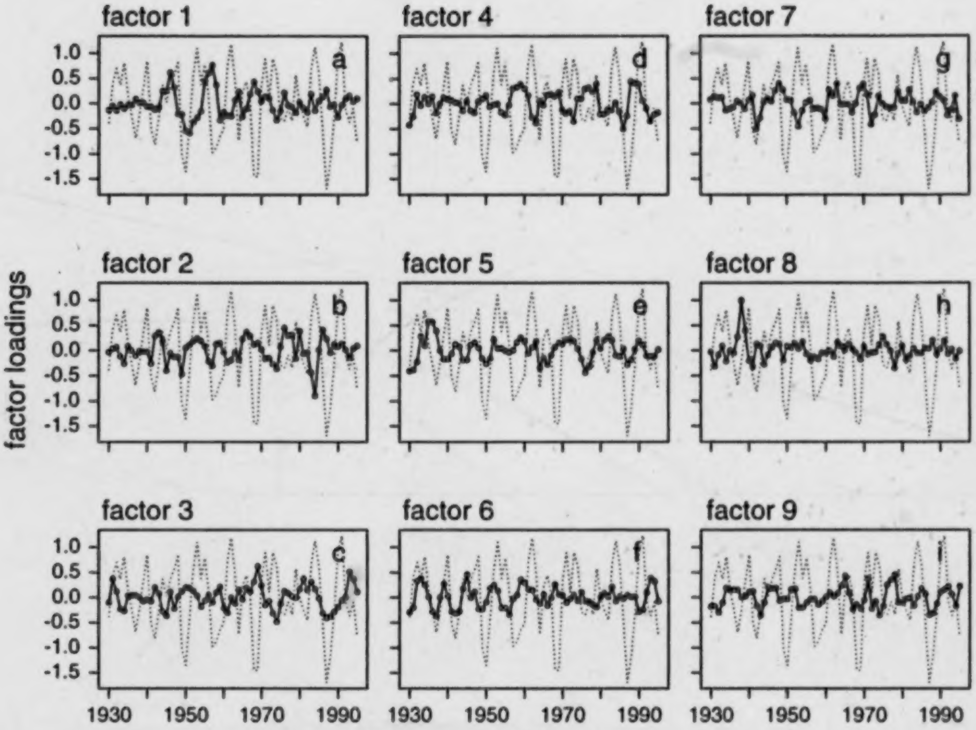

Figure 6.23. Temporal loadings from unrotated T-mode spatiotemporal factor analysis of aspen ring width chronologies from the Cooking L. municipal grid. Dotted line indicates factor 1 scores from S-mode analysis in Fig. 6.15.

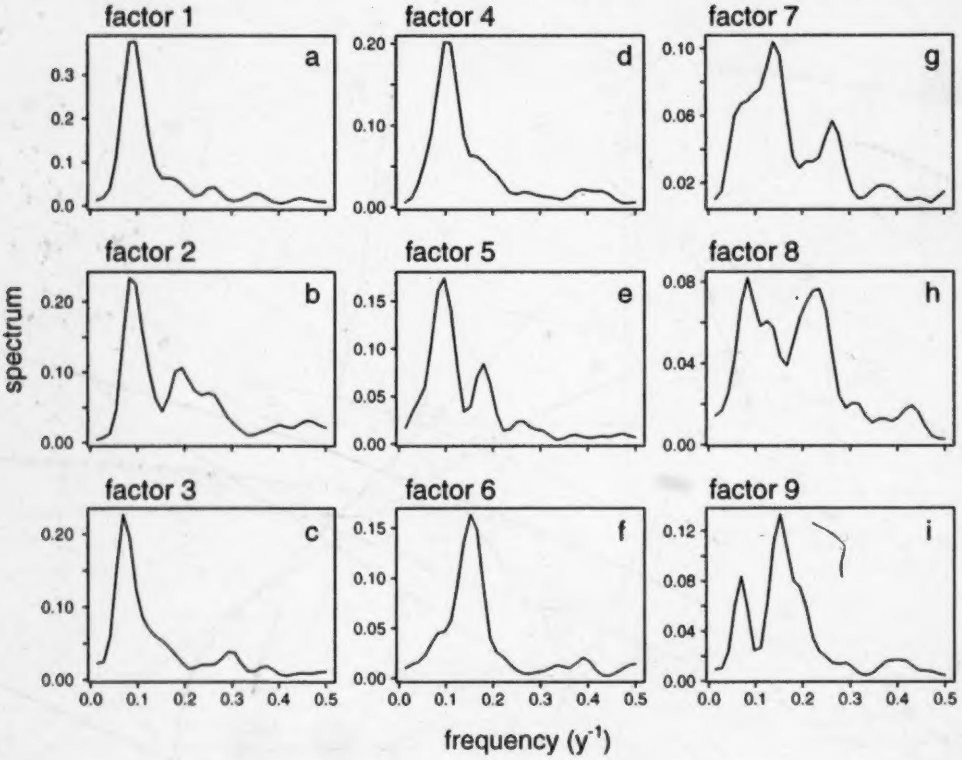

Figure 6.24. Spectra of temporal loadings from unrotated T-mode factor analysis of aspen ring width chronologies from the Cooking L. municipal grid, shown in Fig. 6.23.

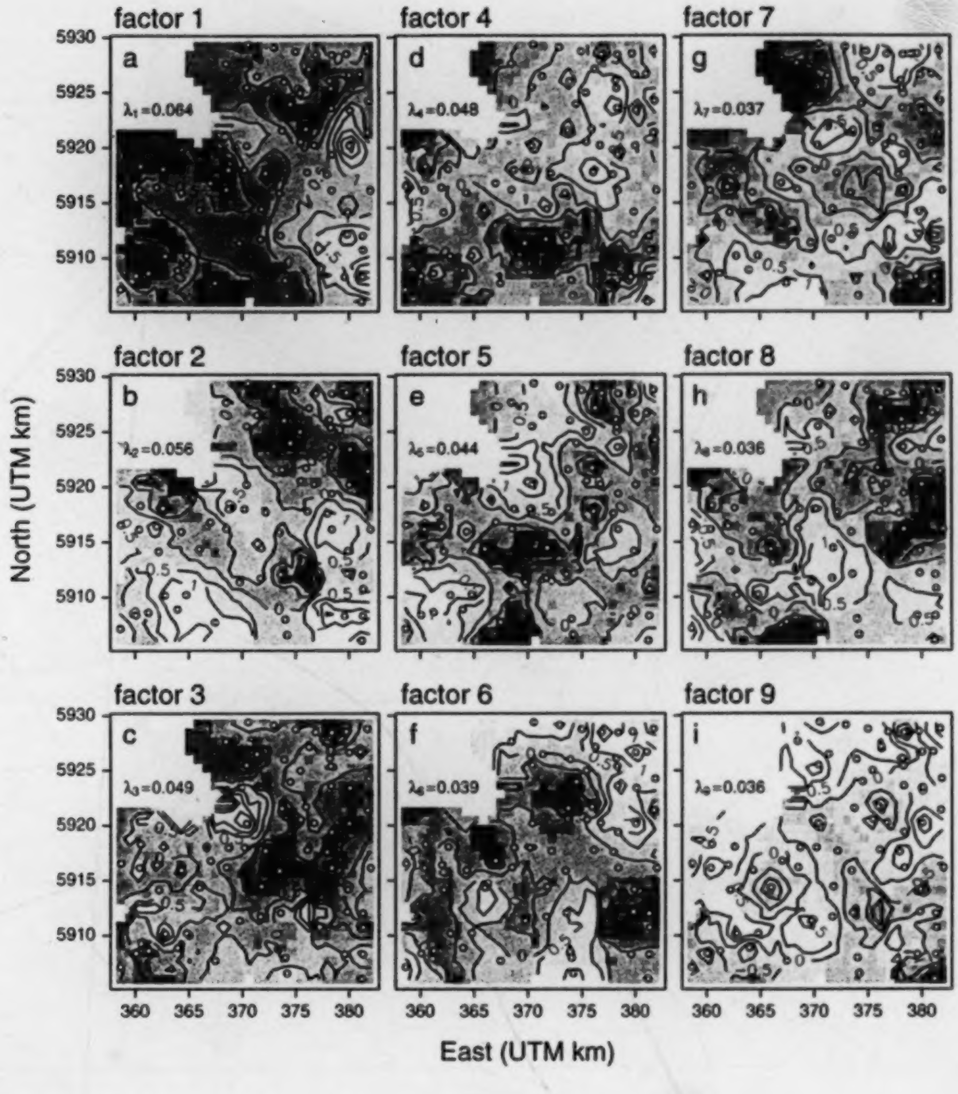
factor 1
a
λ₁=0.064
factor 4
d
λ₄=0.048
factor 7
g
λ₇=0.037
factor 2
b
λ₂=0.056
factor 5
e
λ₅=0.044
factor 8
h
λ₈=0.036
factor 3
c
λ₃=0.049
factor 6
f
λ₆=0.039
factor 9
i
λ₉=0.036
5930
5925
5920
5915
5910
360
365
370
375
380
North (UTM km)
East (UTM km)

Figure 6.25. Spatial scores from unrotated T-mode spatiotemporal factor analysis of aspen ring width chronologies from the Cooking L. municipal grid.

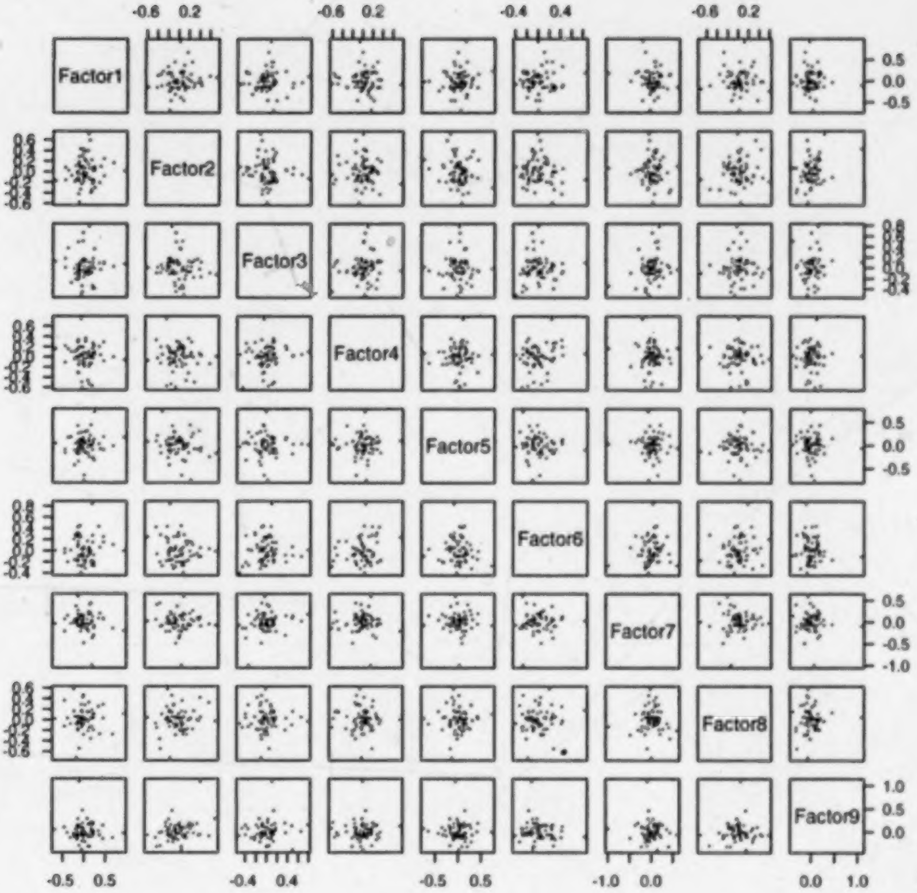

Figure 6.26. Pairwise plots of promax-rotated loadings in Fig. 6.27.

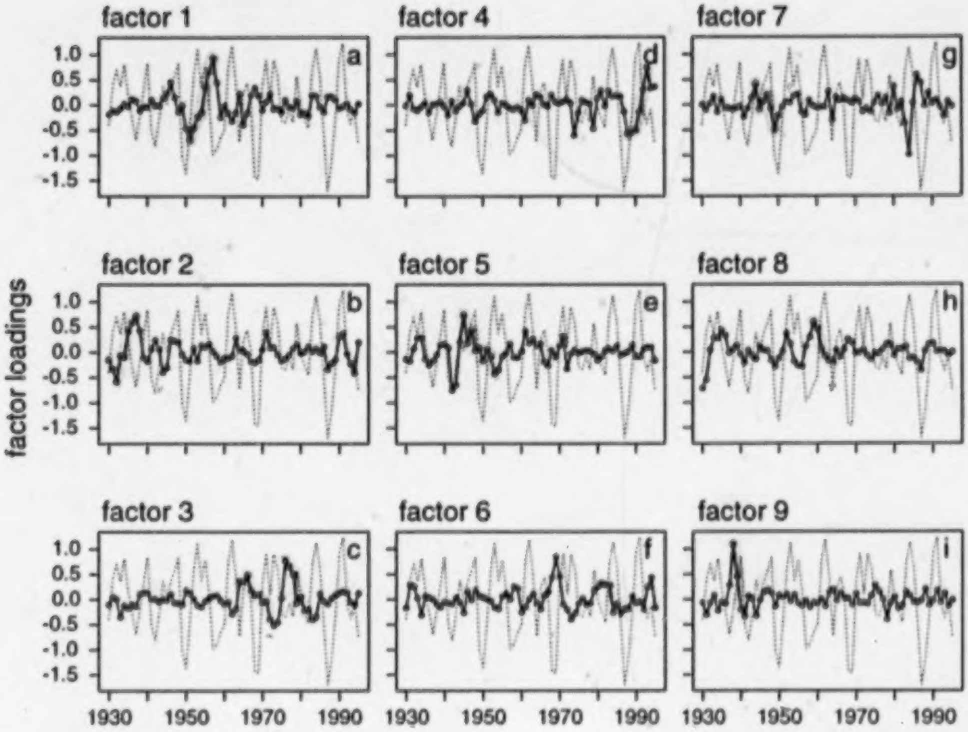

Figure 6.27. Temporal loadings from promax-rotated T-mode spatiotemporal factor analysis of aspen ring width chronologies from the Cooking L. municipal grid. Highlighted segments (numbered) indicate spreading pulses associated with major outbreaks, as described in Table 6.4. Dotted line indicates factor 1 scores from unrotated S-mode analysis in Fig. 6.15.

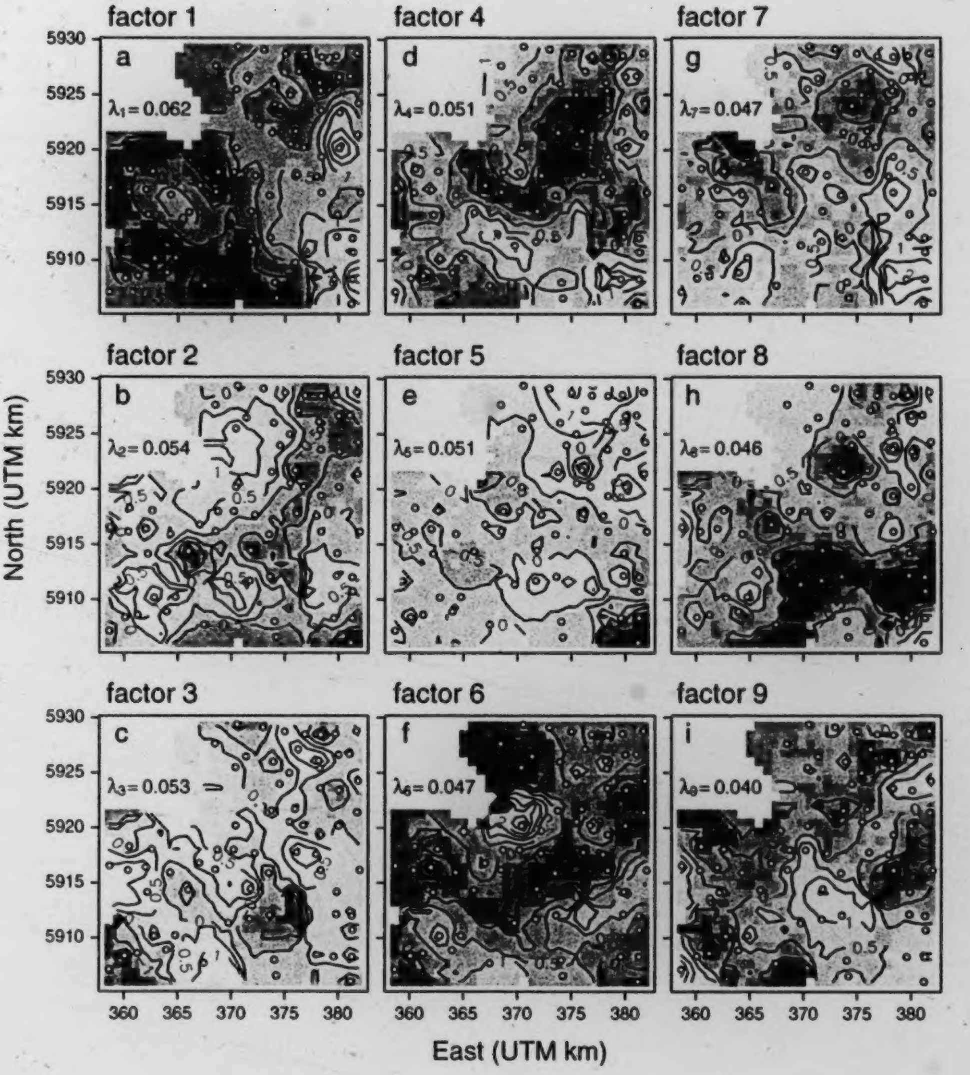
factor 1
a
λ₁ = 0.062
factor 4
d
λ₄ = 0.051
factor 7
g
λ₇ = 0.047
factor 2
b
λ₂ = 0.054
factor 5
e
λ₅ = 0.051
factor 8
h
λ₈ = 0.046
factor 3
c
λ₃ = 0.053
factor 6
f
λ₆ = 0.047
factor 9
i
λ₉ = 0.040
5930
5925
5920
5915
5910
North (UTM km)
360
365
370
375
380
East (UTM km)

Figure 6.28. Spatial scores from promax-rotated T-mode spatiotemporal factor analysis of aspen ring width chronologies from the Cooking L. municipal grid.

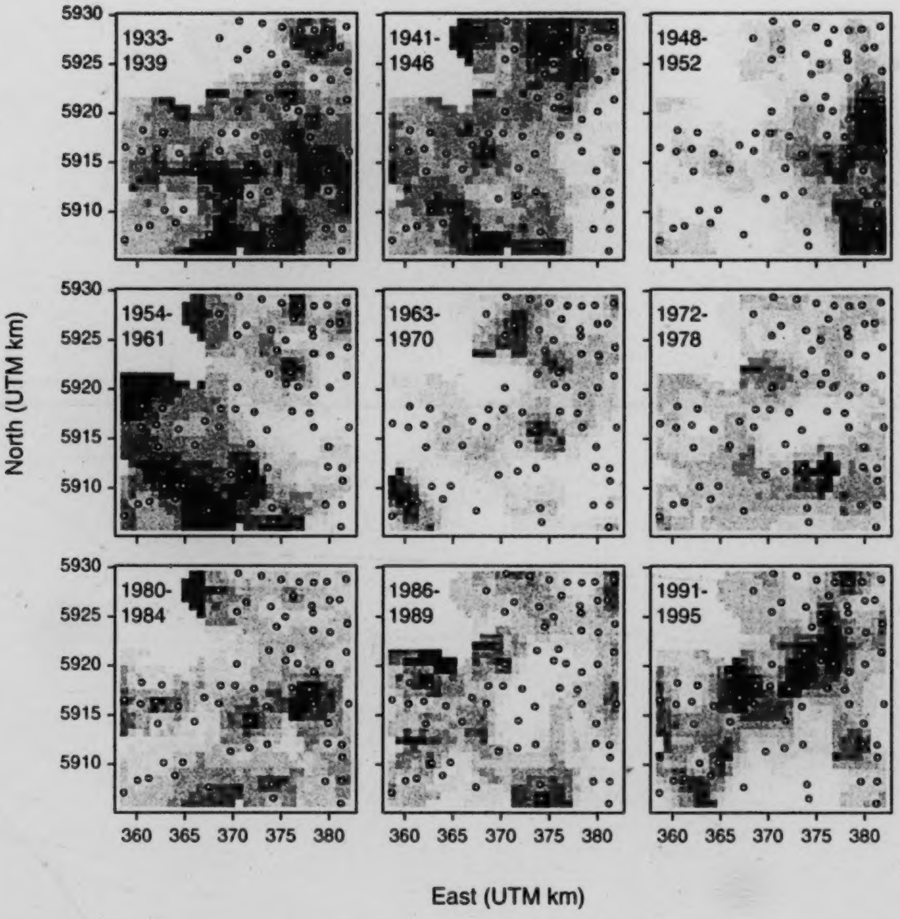
1933-
1939
1941-
1946
1948-
1952
1954-
1961
1963-
1970
1972-
1978
1980-
1984
1986-
1989
1991-
1995
5930
5925
5920
5915
5910
North (UTM km)
360
365
370
375
380
East (UTM km)

Figure 6.29. Mean aspen ring widths across the Cooking L. municipal grid, averaged over nine time frames of varying length. Dark shading indicates relatively low growth. Circles indicate plot locations. Note opposing patterns of disturbance among successive outbreak frames. Correlations among frame-pairs given in Fig. 6.30.

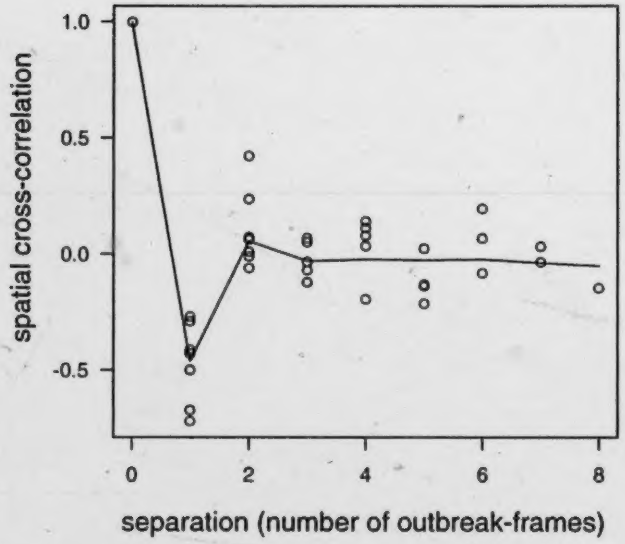

Figure 6.30. Spatial cross-correlation in aspen ring width for pairs of time-averaged growth maps for Cooking L. grid, shown in Fig. 6.29, as a function of separation between frames. Note correlation is strongly negative for successive outbreak pulses, and zero for non-successive outbreaks.

7. THE IMPORTANCE OF DETRENDING ERRORS IN SPATIOTEMPORAL DENDROECOLOGICAL DISTURBANCE RECONSTRUCTION

7.1 Introduction

7.1.1 Detrending in disturbance reconstruction

Tree growth is affected by many dynamic environmental and endogenous factors, but there are certain ecological situations where stem radial growth may be limited principally by a single variable such as moisture or herbivory (Fritts 1976). Dendrochronologists have taken advantage of these situations to reconstruct historical regimes of limiting factors such as precipitation (Meko *et. al.* 1993, Swetnam & Betancourt 1998, Cayan *et. al.* 1998, Cook *et. al.* 1999) and insect defoliation (Swetnam & Lynch 1993). A ubiquitous constraint to accurate dendroecological reconstruction, however, is the pervasive effect of stem, root, and crown density on competition among stems for moisture, light, and nutrients, for such competitive interactions can have a dominating influence on patterns of tree growth (Cook & Kairiukstis 1990).

Recognizing that endogenous stem- and stand-level processes tend to occur on slower time-scales than most environmental regimes, dendrochronologists have used the methods of signal processing to separate the independent effects of endogenous and exogenous limiting factors. It is common practice, for example, to remove the effect of tree-age (which is a proxy of photosynthetic capacity) from a ring width chronology by detrending the series using a straight line, a negative exponential curve, or a stiff spline (Fritts 1976). If the endogenous factors limiting growth fluctuate more dynamically, more flexible splines can be used to detrend the ring width chronology (Cook & Kairiukstis 1990). Of course, the term "detrending" can be misleading if flexible splines are used to remove low- and mid-frequency growth variation.

The effectiveness of detrending in removing endogenous variation rarely needs to be addressed because most low-frequency variability can be attributed to endogenous noise, while the higher-frequency variability usually comprises the exogenous signal of interest. Yet there are situations where the spectral properties of signal and noise overlap. When this occurs, dendroecological reconstruction can be a challenging endeavour, and it becomes important to evaluate, if not the effectiveness of detrending, then the sensitivity of reconstructed patterns to various detrending methods.

7.1.2 Origin of detrending error and bias

With most tree species, exogenous disturbance contributes to mid- and high-frequency variability in ring widths, while endogenous stem and stand processes contribute to non-stationarity and low-frequency variability. But for tree species with exploitive growth habits, the endogenous sources of variability may be of a higher frequency and the exogenous sources of variability may be of a lower frequency. Aspen, for example, grow clonally and are generally moisture- and nitrogen-limited (Peterson & Peterson 1992), such that some of the low-frequency variability in stem growth may be a result of exogenous environmental influences, and some of the high-frequency variability could be a result of endogenous stem, clone, and stand dynamics.

In addition, sudden shifts in mean growth rates could result from changes in resource allocation or recurrent episodes of self-thinning and subsequent canopy closure. Such non-stationarity can not be removed with stiff curves if changes in growth rates are too abrupt. To accommodate such non-stationarity, flexible curves are required. The problem is that detrending with a very flexible curve will inadvertently remove a portion of the exogenous signal one is attempting to retain. The problem with stiff curves could be circumvented through the customized fitting of piece-wise curves; however, this is a highly subjective process and parameter choices may be difficult to justify.

Choosing an appropriate detrending method involves characterizing the spectral properties of the exogenous "signal" to be retained and the endogenous "noise" to be removed, and then choosing a detrending curve (*e.g.* a spline or digital filter) that maximizes the amount of signal relative to noise. If one has no prior understanding about the sources of variability affecting annual growth rates, one must make educated guesses about what constitutes signal and what constitutes noise. Then, based on the assumed spectral properties, one chooses a method that maximizes the separation of signal and noise. In practice, the choice of a detrending method is usually made in partial ignorance of the true nature of signal and noise, and so the choice typically entails guessing how much error is involved and deciding if that level is acceptable. Signal estimation error resulting from incorrect detrending methods is what is referred to as *detrending error*.

Even when the endogenous and exogenous sources of variability are well understood, perfect separation of signal and noise is typically not possible. Indeed, the maximum possible separation between signal and noise is limited by the degree of overlap in their spectral properties. In an ideal situation, where exogenous disturbances have little low-frequency variability, a flexible spline will remove little of the variation due to signal, leading to low detrending error, and an unbiased estimate of signal and noise. But where exogenous disturbances have substantial low-frequency variability, a flexible spline will remove most of the low-frequency, endogenous noise and some of the low-frequency signal, leading to higher detrending error, and estimates of signal and noise that are biased in both amplitude and frequency.

Because any filter will engender detrending error, the choice of detrending method is largely a matter of deciding the quantity and quality of noise one is willing to tolerate in an extracted signal and how much signal one is willing to lose to extracted noise. To the extent that detrending is conservative (retaining some noise in signal and discarding only pure noise) or liberal (discarding some signal in noise and retaining only pure signal) the detrending error will systematically favour a biased signal/noise structure. Thus arises the inevitable problem of *detrending bias*.

7.1.3 Detrending bias in aspen chronologies

7.1.3.1 Choice of detrending method

Aspen ring width patterns can vary tremendously among stands. All of the stand-level chronologies from the Cooking L. municipal grid have significant decadal variability resulting from decadal drought and defoliation by forest tent caterpillar (*e.g.*

Fig. 7.1). However the decadal component of variation is more obvious in stationary chronologies (Fig. 7.1, left column) than in non-stationary chronologies (Fig. 7.1, right column). The aspen chronologies on the left in Fig. 7.1 appear to be sufficiently stationary that they may provide a clear enough indication of defoliation and drought dynamics without detrending. In contrast, the low-frequency variation in the chronologies on the right in Fig. 7.1 is unlikely to be a result of either drought or insect defoliation. Note how non-stationarity and low-frequency variability resulting from endogenous noise can take many forms.

The critical question is: what is the best method for detrending such data? The choice of method may be relatively unimportant when the data are stationary (Fig, 7.1, left column); however, it is a crucial matter when the data are highly non-stationary (Fig. 7.1, right column). Without knowing what factors are driving the variation in aspen ring widths it is difficult to say how these series should be detrended to minimize detrending bias and it is furthermore impossible to measure the effectiveness of detrending in removing noise and retaining signal. As different detrending methods engender different kinds and quantities of detrending error, a range of detrending methods should be examined in terms of their effects on inferences made in subsequent analyses.

In chapter two, the choice of a detrending method for aspen ring width chronologies was based on the hypothesis being tested. There, a conservative test was sought for the hypothesis that defoliation by forest tent caterpillars was the dominant factor limiting aspen growth. Consequently it was purposefully decided to use a detrending method that would bias the statistical test in favour of the alternative hypothesis that growth was more limited by temporal fluctuations in moisture availability. Accordingly, raw aspen ring width chronologies were detrended using successive cubic splines with 50% frequency responses of 50 y and 25 y. These curves are relatively flexible in the sense that they allow for several humps in a century-long record and such severe non-stationarity is rarely observed in tree-ring studies (Cook & Kairiukstis 1990); however, they are relatively stiff compared to the degree of non-stationarity commonly observed in trembling aspen (Fig. 7.1, right column). The reason for detrending these aspen chronologies with flexible splines was to obtain a stationary series of ring widths, especially with respect to the decadal frequency range, such that the likelihood of detecting a significant association with decadal drought was enhanced. This would increase the probability of having to accept the drought-limitation hypothesis and having to reject the defoliation-limitation hypothesis.

These detrending splines were sufficiently flexible that a substantial portion of super-decadal variation was also removed, and some of this may have been due to super-decadal variability in defoliation associated with forest tent caterpillar outbreak. For example, detrending with a flexible spline with a 25 y frequency response may remove variability attributable to both signal (forest tent caterpillar defoliation) and noise (endogenous growth trends), leading to a signal estimate that is lower in amplitude and higher in frequency than the true signal. A similar effect would occur if the chronologies in Fig. 7.1 were detrended with the stiffer of the LOWESS curves shown there. Detrending with the more flexible LOWESS curves shown in Fig. 7.1 would lead to an even larger reduction in amplitude and increase in frequency. These systematic biases in signal estimation led to a certain amount of detrending bias whose magnitude is unknown.

7.1.3.2 Minimizing detrending bias

The importance of detrending bias can be minimized by increasing sample size such that detrending errors in one direction are offset by errors in the other direction. Here the contemporaneous environmental signal is effectively amplified by reducing endogenous noise.

It is because sample sizes were large that detrending bias was not a problem in the temporal analyses of mean aspen ring width chronologies in chapters two, three and five. In the spatiotemporal analysis of chapter six, however, the effective sample size was much smaller. With only two or three trees per stand, detrending bias was not "ironed out" of the stand chronologies, and detrending bias might have influenced the results of subsequent analyses.

7.1.3.3 Spatially structured detrending bias

Of course, both endogenous and exogenous processes have a spatial component. This spatial component is inconsequential in a temporal analysis, but may be relevant when the goal is to decompose a spatial array of dendrochronological data into exogenous spatiotemporal signal and endogenous spatiotemporal noise. Here, any biases inherent in local detrending will have larger-scale implications.

When a single detrending technique is applied uniformly to all stands, detrending bias will vary spatially as a result of spatial variation in exogenous disturbance regimes and endogenous processes. If the signal/noise structure were to vary randomly from stem to stem, spatial variation in detrending bias would be a less critical issue. However, because disturbance regimes and forest-level endogenous processes are likely to be increasingly dissimilar with increasing distance between stems, there is good reason to suspect that signal/noise structures tend to vary as a spatial gradient. To the extent that low-frequency endogenous and/or exogenous components vary systematically through space, so will the detrending bias.

This suggests that the frequency response of detrending splines should be free to vary as a function of stem-level variation in the signal/noise structure. But when the signal/noise structure is not known, it is unclear how the frequency response of the detrending spline should vary from stem to stem. The problem becomes increasingly important with large-scale studies because it is even more likely that the signal/noise structure will vary spatially. If, in addition, the spatial scale of disturbance similarity is unknown, then it becomes rather difficult to decide the extent to which the detrending scheme should vary in space.

With so many unknowns, the rule of parsimony suggests the uniform application of a single detrending spline to all stem-level data may be as good a strategy as any other more complex scheme. Indeed, this is a standard argument and it is the reason this strategy was employed in chapter two. But this simple strategy may be insufficient for the purpose of extracting spatiotemporal structure, as the quality of separation between noise and signal will vary spatially (*i.e.* local detrending bias may not be minimized).

The concern about detrending bias in the spatiotemporal analysis of aspen growth in chapter six is heightened by the fact that aspen stems vary in their vulnerability to detrending error (Fig. 7.1). Those stems with relatively stationary ring-widths (Fig. 7.1, left column) require little detrending. Here, the amount of detrending bias will be small and will not vary greatly in response to the flexibility of detrending. Those stems with a large proportion of low-frequency noise (Fig. 7.1, right column) will lose much variability to detrending. Here, detrending error will not only be higher, it will also be sensitive to the degree of flexibility in detrending.

If stands closer together are more similar in their non-stationarity, this could lead to spatially structured detrending bias. The problem is that this would appear as coherent spatiotemporal variability that could be falsely attributed to asynchronous disturbance. In fact, the problem is worse than this because the detrending error is temporally patterned, and the magnitude of patterning can be quite strong, as the next section demonstrates.

7.1.3.4 Periodicity in correction errors

Detrending bias can engender both positive and negative detrending errors within a chronology. For example, detrending a quasi-periodic chronology with a spline of low-frequency response will lead to resonance effects over some mid-frequency range. Fig. 7.2 illustrates how correction errors may oscillate from positive to negative values within stand-level aspen chronologies. Consider the dips in aspen growth at 1937 and 1942 in stand 21. Notice how detrending would affect the pattern of oscillation in corrected ring widths. With the flexible detrending curve, each corrected dip would appear to be of similar magnitude. With the stiff detrending curve, the first would appear much smaller than the second. One of these reconstructions is more correct than the other, but it is not known which. If the two disturbances were in fact equal in magnitude (as suggested by the seemingly stationary chronologies of Fig. 7.1), then detrending with the stiffer curve would lead to an alternating pattern of over-correction for the 1937-1938 dip and under-correction for the 1942-1943 dip. Notice how correction of dips at 1948-1950 and 1957-1960 in stand 21 would be equally problematic, generating an alternating pattern of under-correction followed by over-correction.

The same effect would occur in other aspen chronologies and in other years (Fig. 7.2). Two general observations are relevant here. First, the pattern of detrending bias would be especially strong for the pair of dips in 1986-1989 and 1992-1994. In all four chronologies, the first of these dips would be somewhat reduced and the second would be substantially reduced. This, however, would be an artifact of the chronologies terminating in a year of forest tent caterpillar outbreak when growth was being suppressed. Had sampling been conducted some years later, growth rates might have recovered, as they did a few years earlier in stands 36, 37, 125 (Fig. 7.1). This suggests that all the chronologies from the Cooking L. municipal grid are non-stationary in signal/noise structure and that detrending with any method unfairly attributes signal to noise in the latter part of the chronology. Second, the pattern of low-frequency non-stationarity varies among stands such that the magnitude and the pattern of alternating detrending bias varies among stands. At stand 20, for example, the artificial induction of periodicity in corrected ring widths would be especially strong (Fig. 7.2, bottom). Uncertainty in correctness of detrending thus leads to a certain inevitable artificial amplification of periodicity in some frequency range.

Periodicity in detrending errors is not critical when many detrended chronologies are being averaged, for here the detrending errors tend to cancel out. But when only a few samples are being averaged, the errors will rarely balance each other. The crucial point is this: if there is systematic spatial structure in the periodic pattern of detrending error, *spatiotemporal analysis will uncover this coherent structure and it will be indistinguishable from joint spatiotemporal variability associated with spreading patterns of disturbance.*

The specific concern of the present study is that apparent sub-decadal outbreak asynchrony revealed in chapter six was an artifact of spatially structured periodic detrending error. At issue is whether such an effect could arise from systematic spatial variation latent in the signal/noise structure. The foregoing qualitative analysis suggests that danger is quite high.

7.1.5 Objectives of the current study

The purpose of this chapter is to analyze the sensitivity of spatiotemporal structure in extracted dendroecological signals to the frequency response parameter used in detrending. The specific objective is to determine to what extent disturbance asynchrony revealed in aspen ring width chronologies from the Cooking L. municipal grid in chapter six might be an artifact of spatially structured periodic detrending bias resulting from a spatially varying signal/noise structure.

The matter is important to resolve because the inferred patterns of forest tent caterpillar outbreak asynchrony in chapter six are remarkable in that they are difficult to reconcile with predictions from theoretical host-parasitoid models. Given that such patterns are theoretically unlikely, they should be scrutinized closely with a very critical eye.

7.2 Methods

7.2.1 Data source

Of the 128 aspen ring width chronologies from the Cooking L. municipal grid, 76 spanned the period 1929-1994. Non-detrended ring widths from these partial stem-wise chronologies were averaged for each stand, and these non-detrended partial stand-wise chronologies were submitted to a variety of detrending treatments.

7.2.2 Data analysis

All analyses were conducted with the R statistical package, version 1.2.1 (Ihaka & Gentleman 1996, Hornik 2001).

7.2.2.1 Detrending

Non-detrended partial stand-wise chronologies were detrended by fitting LOWESS functions (Cleveland 1981) and subtracting the fitted values from the original non-detrended data. The flexibility of detrending was varied from extremely rigid to extremely flexible by setting the smoothing parameter to the values: {1.0, 0.5, 0.2, 0.1}. The detrended signals estimated by this procedure were the primary object of study.

Note the method of detrending used here differed in three fundamental ways from that employed in chapter two: (1) stand-wise chronologies were detrended instead of stem-wise chronologies; (2) partial 66-year chronologies were detrended instead of whole chronologies; (3) LOWESS curves were used for detrending instead of cubic splines. The results of this chapter, however, do not hinge on these procedural differences.

7.2.2.2 Spatiotemporal factor analysis

The non-detrended data were analysed using unrotated factor analysis in order to demonstrate the existence of spatially structured low-frequency variability resulting from endogenous sources, possibly in interaction with exogenous disturbances. Nine factors were extracted.

7.2.2.3 Spectral analysis of extracted signals

The mean chronology of the 76 locally extracted signals was computed for each detrending treatment and these were submitted to spectral analysis (Chatfield 1989). The objective was to illustrate the effect of varied detrending flexibility on periodicity in the resulting global mean signal.

7.2.2.4 Spatiotemporal autocorrelation in conditional time-averages

Spatiotemporal factor analysis of detrended data having suggested that outbreaks might be well-organized over time-scales longer than a single year (chapter six), annual growth maps over the period 1929-1994 were averaged over a number of years. Nine temporal frames varying in length from four to nine years were used to summarize spatial patterns in nine major disturbance pulses. The frame boundaries were chosen based on results in chapter six. To avoid introducing framing bias, frame boundaries were chosen such that years of peak growth in 1940, 1947, 1953, 1962, 1971, 1979, 1985, and 1990 were not included in the analysis.

To determine whether growth maps in a given frame were consistently related to growth maps in previous frames, spatiotemporal autocorrelation functions were constructed by computing spatial correlations between successive growth-map frames, for frames separated by two disturbance episodes, etc. To determine the influence of detrending on spatiotemporal structure in extracted signals, this was done for non-detrended data as well as the various detrended data sets.

7.3 Results

7.3.1 Spatiotemporal factor analysis

The first two factors, which explained 19.5% and 12.7% of the total variation in the non-detrended data, exhibited very low frequency trends in temporal loadings (Fig. 7.3) and large-scale gradients in spatial scores (Fig. 7.4). Factor one contrasted stands on the basis of whether long-term annual growth rates were higher in the early or late portion of the chronology, while factor two contrasted stands on the basis of the long-term mid-chronology growth rate (Fig. 7.3). The other seven factors accounted for 29.7% of the total variation and loading patterns did not exhibit nearly as much low-frequency variation (Fig. 7.3).

There were some higher frequency components in factor one and two loadings (Fig. 7.3). Factor one showed minor peaks around 1942, 1949, and 1957, which were years of outbreak disturbance (chapter two). It appears that factor one, then, may represent a weak relationship between non-stationary trends in baseline growth rates, and stand disturbance history. Specifically, it appears that stands defoliated during those episodes tended to go into decline (black patches in Fig. 7.4a), while those that were not defoliated did not go into decline. Factor two can be interpreted the same way with respect to defoliating disturbances in 1968-1969, 1978-1982, and 1987-1988, and rapid decline thereafter.

7.3.2 Spectral analysis

The non-detrended data showed substantial low-frequency variability (Fig. 7.5a,f) and this was not removed by detrending with a nearly linear curve (Fig. 7.5g). By increasing the flexibility of the detrending curve, however, mean chronologies became increasingly stationary in mean and variance (Fig. 7.5c,d,e) and exhibited lower amplitude fluctuations, with a greater proportion of variation coming from the middle of the frequency spectrum (Fig. 7.5h,i,j).

7.3.3 Spatiotemporal autocorrelation in conditional time-averages

When non-detrended aspen growth maps were averaged across temporal frames of varying sizes (between four and eight years long), areas of high growth appeared to occur on the same parts of the study area between successive disturbance frames (Fig. 7.6). In fact the spatial correlation between successive disturbances was strongly positive for successive disturbances, but swung to negative values for disturbance separated by 4, 5, or 6 episodes (Fig. 7.5k).

The relationship between spatial correlations and temporal frame-separation changed with increased flexibility of detrending. Nearly linear detrending suggested successive disturbances were uncorrelated but that disturbance episodes two frames apart were negatively correlated (Fig. 7.5l). With the smoothing parameter set to f=0.5, successive disturbances were negatively correlated, but the correlation damped to zero for disturbance episodes separated by three or more frames (Fig. 7.5m). Increasing the flexibility of the detrending curve beyond these caused disturbances separated by one or more frames to be uncorrelated (Fig. 7.5n,o).

Notably, when the data were detrended using the set of curves generated by setting the smoothing parameter to f=0.5, decadal variability in the extracted signal was maximized (Fig. 7.5h) and the spatiotemporal pattern of disturbance (Fig. 7.7) most strongly resembled the pattern of sub-decadal asynchrony revealed in chapter six (Fig. 6.29).

7.4 Discussion

Detrending with increasingly flexible LOWESS curves tends to remove a wider range of low-end variability from the target signal. It is unclear how much of this variability is actually attributable to endogenous growth trends and how much is due to super-decadal variability in exogenous disturbances. Some of this low-frequency variability may even be a result of interactions between endogenous and exogenous processes. In particular, patterns of stand decline may relate to forest tent caterpillar outbreak history (Hogg & Schwarz 1999).

Without knowing the nature of the signal/noise structure, it is difficult to determine how much bias might be associated with a given detrending scheme. The best way to solve this problem might be to determine the nature of the endogenous growth variation by studying growth patterns of undisturbed aspen. Then these patterns could be used to guide the detrending procedure.

Without knowing how the signal/noise structure varies in space, it is possible that sub-decadal disturbance asynchrony is completely an artifact of spatially structured periodic detrending errors. If this is the case, then an explanation is required for the low-frequency variability revealed in factors one and two from the spatiotemporal factor analysis. For example, though it seems unlikely, there is a small chance this could be due to low-frequency variability in tent caterpillar abundance. It is more likely, however, that these are non-stationary growth trends resulting from sudden release, in association with pulses of stem mortality caused by outbreaks and drought, followed by age-dependent decline.

The fact that results from spatiotemporal analysis in chapter six are sensitive to the choice of detrending method suggests that there are limits to its applicability when spatial replication is low. At the same time, the fact that spatiotemporal analysis was powerful enough to detect such structure is an encouraging sign that it is a useful approach to summarizing spatiotemporal structure in disturbance patterns. The usefulness of this technique could be increased by sampling much more intensely than at the rate of three trees per stand, which was the sampling intensity used here. This would provide a better estimate of the noisy endogenous component one intends to remove by detrending.

Detrending dendrochronological data is a standard procedure, but rarely is much thought given to the influence of detrending bias on spatiotemporal structure revealed in the extracted signal. This study shows why the choice of detrending technique must be given careful thought if the objective is spatiotemporal analysis of disturbance patterns. The issue is irrelevant in purely temporal analyses simply because the question of disturbance spread patterns can not be asked.

7.5 Conclusion

This study illustrates how spatially structured bias in periodic detrending errors could arise and it shows that spatiotemporal factor analysis may not be able to distinguish such bias from spatiotemporal variability associated with recurring, spreading disturbances. At the same time, this study provides no proof that this must be so. This issue can only be addressed through formal mathematical investigation into the effect of spatially structured periodic detrending error on the ability to detect patterns of disturbance spread with spatiotemporal factor analysis.

More specifically, it appears sub-decadal outbreak asynchrony revealed in spatiotemporal analysis of aspen ring width chronologies in chapter six could easily be an artifact of detrending with stiff splines. To evaluate the truth of this assertion, however, one needs a better understanding of the actual signal/noise structure. This would require additional sampling. Given how incompatible these asynchronous outbreak patterns are with predictions from theoretical host-parasitoid models, and the important implications for empirical forecasting, the matter merits further attention. Until such time, these patterns should be viewed with great skepticism.

In general, there are several ways to minimize the influence of detrending errors on results derived from spatiotemporal analysis:

1. To minimize the impact of detrending bias in the latter part of a chronology, one should wait until disturbance episodes have terminated and growth rates have

rebounded before sampling.

2. By increasing the number of samples per chronology to something between ten and twenty, it should be possible to reduce stand-level detrending bias to acceptable levels. For trees that grow clonally, it may be necessary to sample more than one stand per chronology. Five stands per chronology with three trees per stand may be sufficient to get stem- and stand-level detrending biases to cancel at the chronology-level. For the reconstruction of tent caterpillar outbreaks from trembling aspen, this would imply a five-fold increase in sampling intensity.

3. Additional studies of undisturbed growth would provide a clearer picture of the endogenous noise one wishes to remove. Similarly, a precise record of stem-level defoliation would provide a clearer picture of the exogenous signal one wishes to retain. Knowledge here could be used to design optimal signal-processing filters.

4. Customized stand-level detrending, though unparsimonious, may be justifiable - especially if subjectivity could be eliminated. This could be accomplished by designing objective procedures to minimize spatiotemporally coherent detrending errors.

It is conventional dendrochronological wisdom that stiff cubic splines offer a conservative method for detrending dendrochronological data. This may be the case when they are used to detrend a large number of stem-level chronologies comprising a single mean chronology, which will be analysed temporally; however, it is not necessarily so when the stem-level chronologies comprise a spatial array of chronologies that will be analysed spatiotemporally. Thus a detrending technique that is conservative in a temporal context may be liberal in a spatiotemporal context. When choosing a detrending technique it is important to consider the goals of analysis. For exploratory pattern analysis it may be wise to consider a variety of detrending methods.

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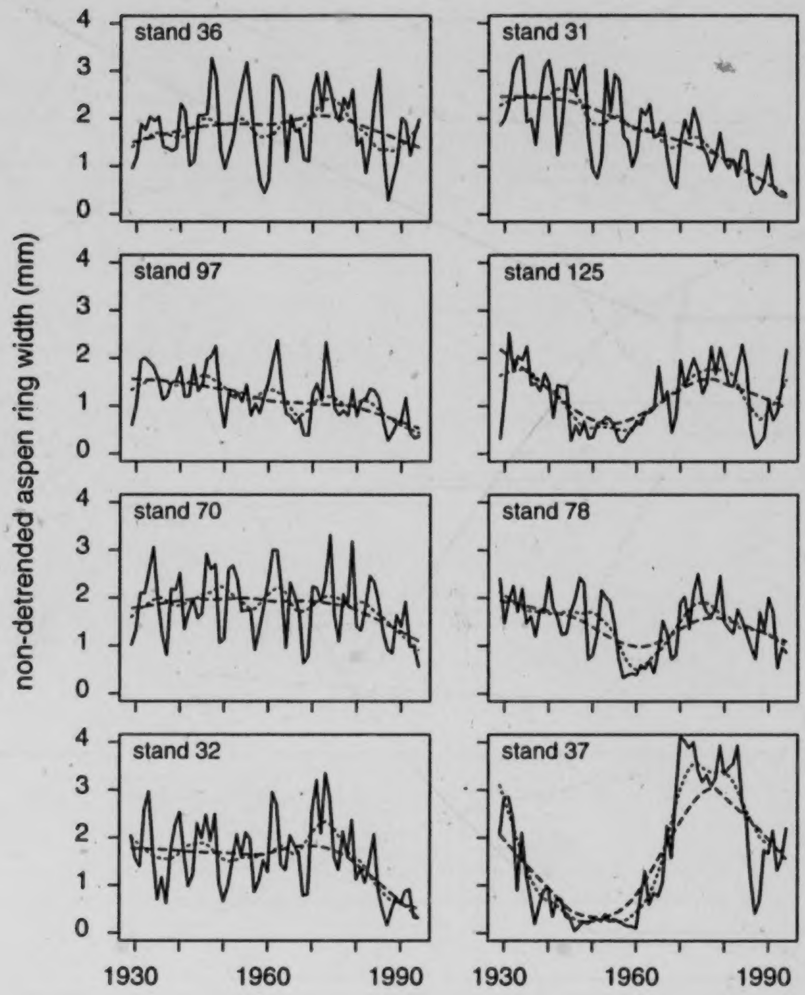


Figure 7.1. Partial chronologies of aspen ring widths for selected stands from the Cooking L. grid. Stiff (f=0.5) and flexible (f=0.2) LOWESS curves shown as dashed and dotted lines respectively. Left column shows stationary chronologies requiring little detrending. Right column shows non-stationary chronologies requiring detrending.

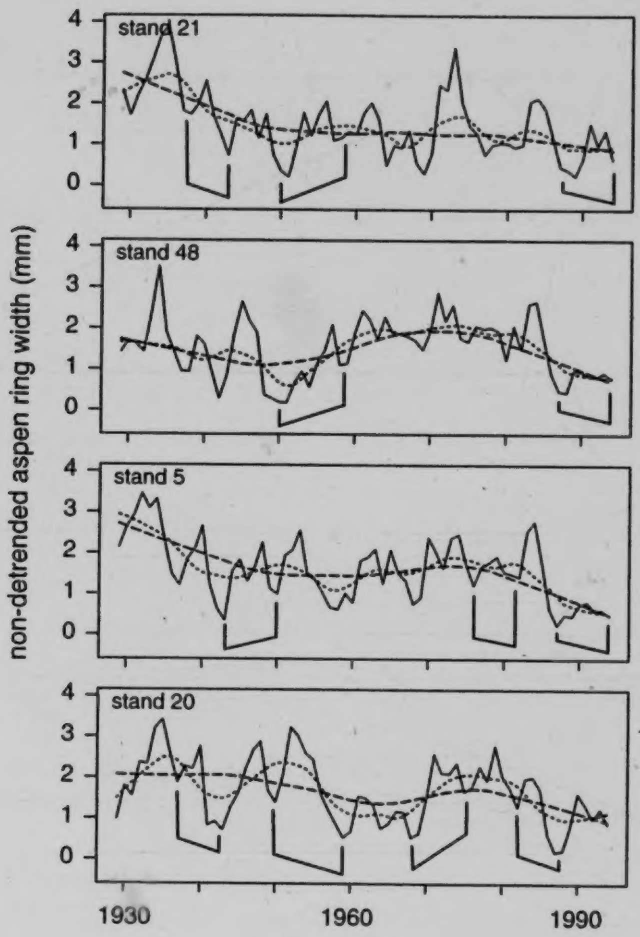


Figure 7.2. Four examples of mildly non-stationary partial chronologies of aspen ring widths that show high local sensitivity to stiffness of detrending curve. Stiff (f=0.5) and flexible (f=0.2) LOWESS curves fitted to each chronology shown as dashed and dotted lines respectively. Markers indicate pairs of sub-decadal dips in aspen growth occurring during non-stationary segments of chrnology where stiff-spline detrending may introduce alternating patterns of positive and negative correction bias among successive dips.

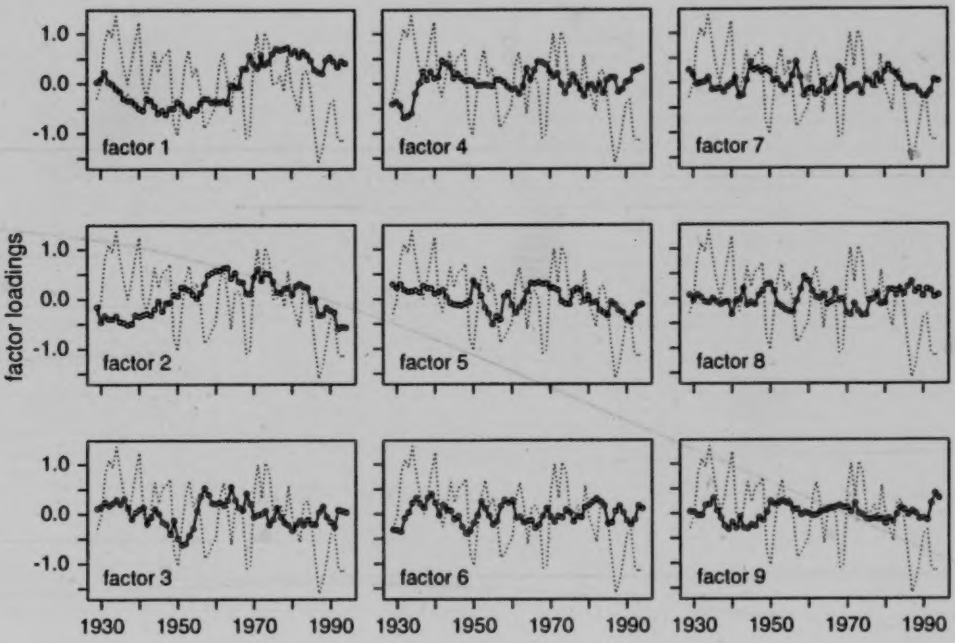


Figure 7.3. Temporal factor loadings from unrotated spatiotemporal factor analysis of undetrended stand-wise aspen ring width chronologies. Corresponding factor scores shown in Fig. 7.4. Scaled mean undetrended ring widths shown as dotted line. Note low-frequency variability in loadings for factors 1 and 2.

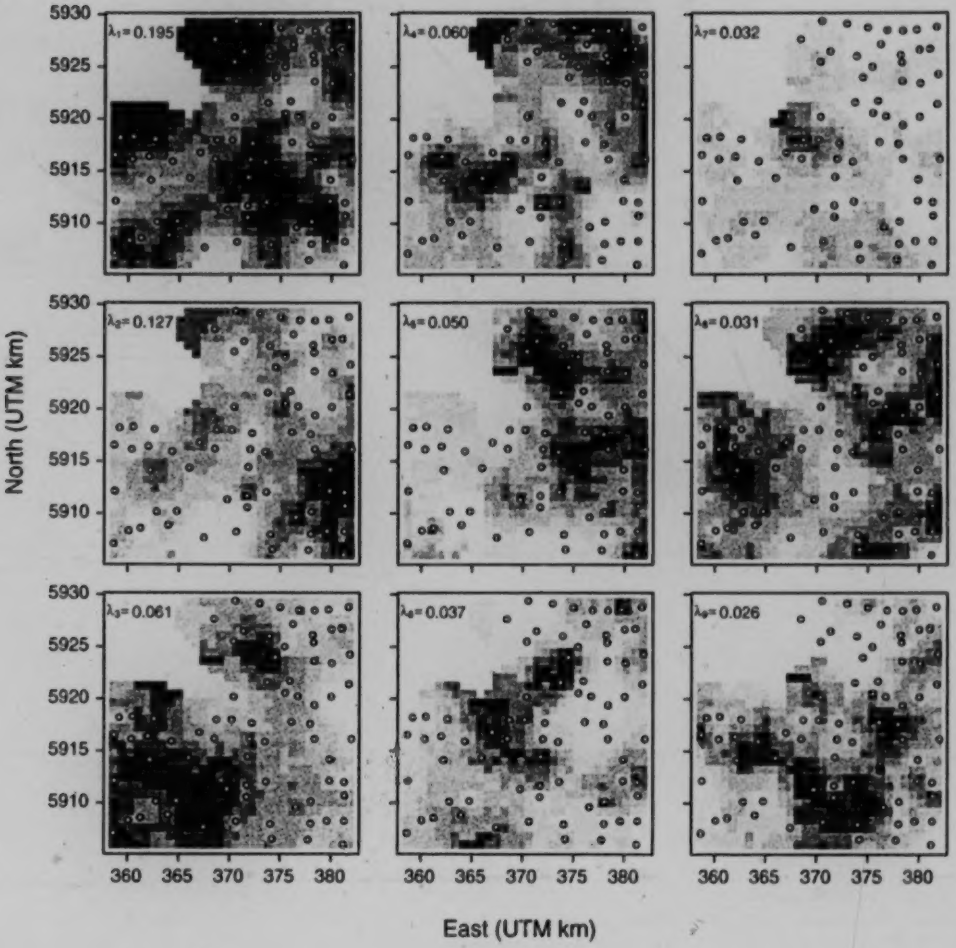

λ₁= 0.195
λ₂= 0.127
λ₃= 0.061
λ₄= 0.060
λ₅= 0.050
λ₆= 0.037
λ₇= 0.032
λ₈= 0.031
λ₉= 0.026
5930
5925
5920
5915
5910
North (UTM km)
360
365
370
375
380
East (UTM km)

Figure 7.4. Spatial factor scores from unrotated spatiotemporal factor analysis of undetrended stand-wise aspen ring width chronologies. Light shading indicates positive scores; dark indicates negative scores. Corresponding factor loadings shown in Fig. 7.3. Proportion of variation explained by each factor, λ, shown in upper left corner. Circles indicate stands included in analysis.

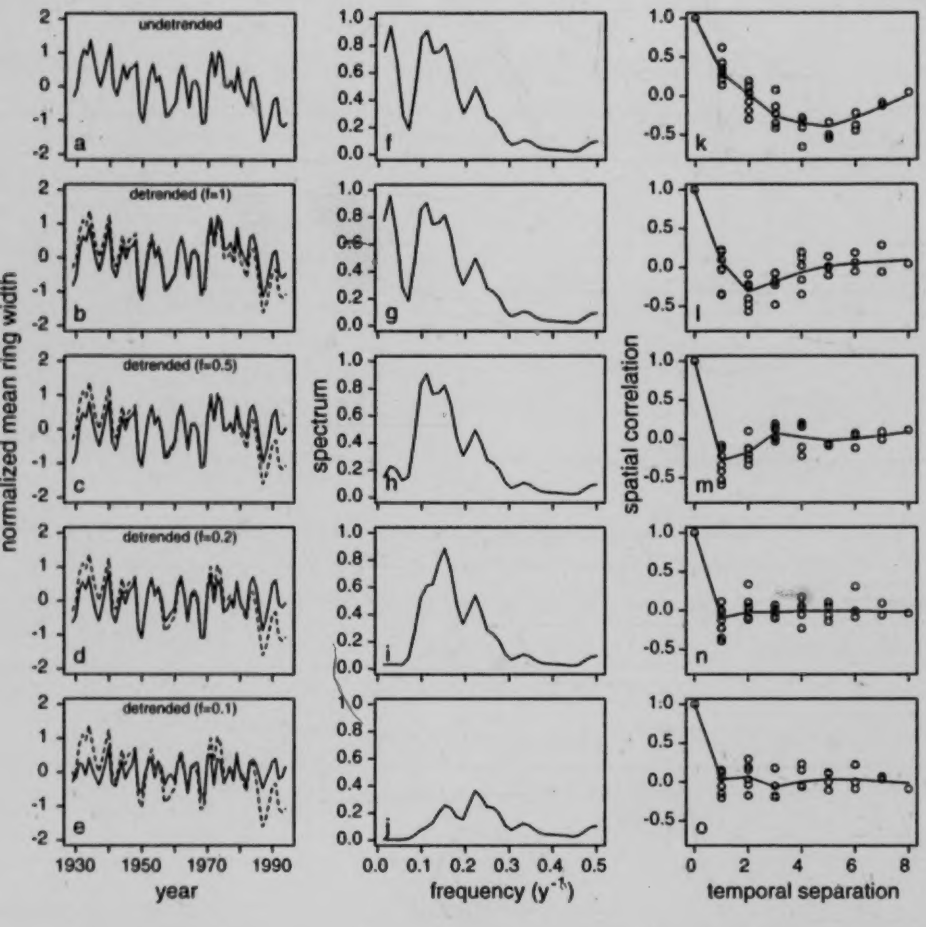
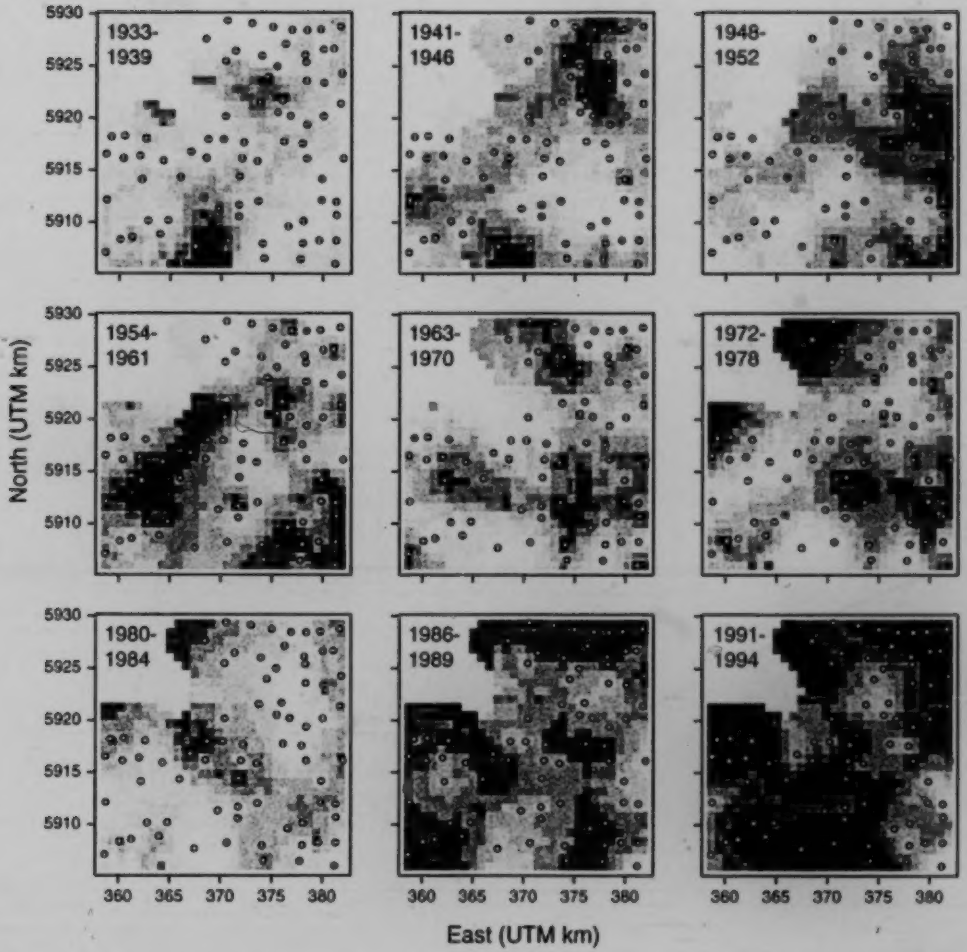


Figure 7.5. Effects of detrending with curves of varying degrees of flexibility. Non-detrended data in top panels. Smoothing parameter, f, is varied from 1.0 to 0.1 in lower panels. Left column: mean detrended ring width chronology, with non-detrended mean chronology shown as dotted line. Center column: spectrum of mean chronology. Right column: spatiotemporal autocorrelation function for time-averaged growth maps separated by an increasing number of disturbance episodes.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East (UTM km)

Figure 7.6. Undetrended aspen ring widths averaged over nine four- to eight-year time frames. Light shading indicates wide rings; dark indicates narrow rings. Frames were chosen such that each represents the occurrence of one major disturbance. High similarity between successive disturbance frames leads to positive correlation in Fig. 7.5k for temporal separation=1. Note negative covariance between maps separated by 4-6 frames. Circles indicate plot locations.

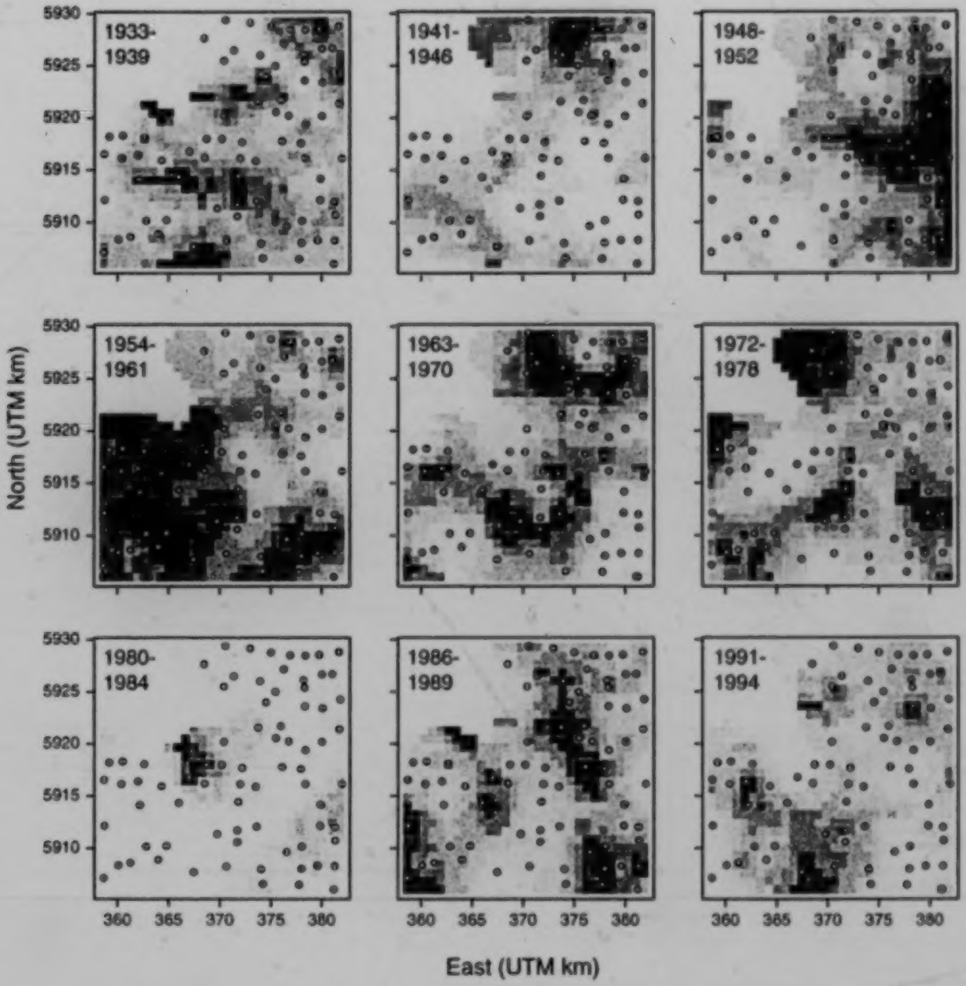
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Figure 7.7. Detrended aspen ring widths (f=0.5) averaged over nine four- to eight-year time frames. Symbols as in Fig. 7.6. High dissimilarity between successive disturbance frames leads to negative correlation in Fig. 7.5m for temporal separation=1.

8. THE EFFECT OF WINTER TEMPERATURE ON FOREST TENT CATERPILLAR EGG SURVIVAL AND POPULATION DYNAMICS IN NORTHERN CLIMATES

8.1 Introduction

The central problem of animal population ecology has been the basis of population regulation and the biological mechanisms by which it may be achieved. In attempting to understand the forces that govern population fluctuations, differing views have emerged regarding the importance of: (1) density-dependent survival and reproduction (Nicholson 1954, Andrewartha & Birch 1954), (2) environmental stochasticity (May 1973, Reeve 1988, Wilson *et. al.* 1998), (3) non-linear dynamics and complex attractors (May 1976, Schaffer & Kot 1985, Berryman & Millstein 1989, Turchin & Taylor 1992, Logan & Allen 1992, Hastings *et. al.* 1993), (4) spatial heterogeneity (Hilborn 1975, Hastings 1977), (5) top-down versus bottom-up processes (Hunter & Price 1992), and (6) non-equilibrium dynamics (DeAngelis & Waterhouse 1987, Hastings & Higgins 1993, Hastings 1998, Kaneko 1998). There is now some agreement as to the terms of debate and the importance of stochasticity and spatial heterogeneity, and there is a consensus that no one explanation is likely to prevail in all systems (Turchin 1995). However, disparate views on the cause of population cycles have persisted (Kendall *et. al.* 1999), especially in regards to periodic insect outbreaks (*e.g.* Martinat 1987, Ginzburg & Taneyhill 1994, Berryman 1996, Myers 1998).

Even among the best-studied systems, such as the spruce budworm, *Choristoneura fumiferana* Clem., there is substantial debate about the nature of population regulation and the cause of outbreaks: are outbreaks caused by an eruptive mechanism whereby regulation about a low-density equilibrium state occasionally fails (Morris 1963, Ludwig *et. al.* 1978, Clark & Holling 1979, Blais 1983, Campbell 1993) or a non-eruptive mechanism whereby populations cycle loosely about a single equilibrium state due to lagged effects of parasitism (Royama 1996b, Berryman 1996) or a gradient involving both types of dynamics (Williams & Liebhold 2000a)?

The case of the forest tent caterpillar, *Malacosoma disstria* (Hbn.), is similar in this regard. A defoliator of broad-leaved trees, primarily trembling aspen (*Populus tremuloides* Michx.), the forest tent caterpillar exhibits occasional population eruptions that are synchronized into large-scale outbreaks (Hildahl & Reeks 1960, Sippell 1962, Hodson 1977, Daniel & Myers 1995). In the heavily forested parts of North America population densities may span four orders of magnitude over the course of an outbreak (Witter *et. al.* 1975).

The natural history and population ecology of tent caterpillars in northern forests is well known and has been summarized before (Hodson 1941, Witter 1979, Ives & Wong 1988, Fitzgerald 1995). Briefly, unhatched pharate larvae pass the winter inside their eggs, which are aggregated into a single band on the tips of twigs. Although cold tolerant, eggs are susceptible to freezing by extreme cold (Wetzel *et. al.* 1973) and the risk of mortality varies seasonally as a result of changes in egg physiology (Hanec 1966) and fluctuations in temperature. In spring, around the time of aspen bud-break, larvae eclose and feed if foliage is available. At this early stage larvae are vulnerable to freezing and starvation (Raske 1975) and entire colonies may be fatally dislodged by windstorms (Blais *et. al.* 1955). Larvae feed colonially for the first four stages, during which time they are subject to parasitism and predation by a vast array of natural enemies including spiders, ants, pentatomids, birds, wasps and tachinid flies (Green & Sullivan 1950, Parry *et. al.* 1997). Living gregariously, the larvae can contract a nuclear polyhedrosis virus, which is often fatal (Stairs 1966). At high densities they are also vulnerable to microsporidian infections, which reduce larval vigour and adult fecundity (Thomson 1959) and persist in populations for generations (Wilson 1980). During the fifth larval stage, entire stands of trees can be completely defoliated, and larvae may wander for sizable distances in search of food and/or pupation sites (Batzer *et. al.* 1995). Surviving larvae spin protective silken cocoons in foliage, and pupate. Many of the non-surviving larvae act as hosts to Dipteran parasitoids. Upon completing larval development, these parasitoids drop to the ground and pupate in the litter, where they pass the winter underneath the snow, and emerge the following spring. Around mid-July, two to three weeks after hosts pupate, sexually mature forest tent caterpillar moths emerge, mate, and the females lay eggs. The flight range of moths has not been measured, but adult females are not known to disperse large distances without the aid of unstable air masses (Brown 1965).

Although parasitoids are ubiquitously associated with the decline of forest tent caterpillar populations, these declines often are initiated by a climatic perturbation and are sometimes associated with local viral epizootics (Hodson 1977, Witter 1979). Repeated defoliation seems not to reduce the quantity of food available *via* stem mortality (Ghent 1958, Churchill *et. al.* 1964). However, larval nutrition and adult fecundity are compromised at population high densities through intraspecific competition (Hodson 1941) and reduced food quality (Dr. J.R. Spence, personal communication). Thus it is unclear to what extent population collapse is caused by density-dependent factors (parasitoids, disease, competition), and whether it is the top-down processes (parasitoids, disease) or bottom-up processes (competition for high quality food) that dominate. Even less is known about the factors that lead to the initiation of an outbreak, although favourable spring weather (Ives 1973) and reduced efficiency of natural enemies (Parry *et. al.* 1997) are commonly suggested. Indeed, it is not even clear whether outbreak dynamics are more analogous to catastrophes generated by a complex attractor, such as a cusp-manifold (*e.g.* Rose & Harmsen 1978, 1981), or to cycles generated by a point attractor, such as that suggested by a classic, linear host-parasitoid interaction subject to random perturbation (Royama 1996b). The nature of regulation remains a mystery.

Andrewartha and Birch (1954) suggested the distribution and abundance of animals was largely determined by environmental factors, which vary in space and time. The notion that animal population cycles are driven by cyclic environmental changes today seems antiquated (Berryman 1996); however the view that species ranges and population boundaries are determined by environmental dynamics is as popular as ever, even in the case of cyclic forest insects. For example, Tenow (1975) described how cyclic populations of autumnal moth, *Epirrita autumnata* (Bkh.), display clear elevational gradients in abundance along mountain-sides in Sweden. Populations on mountain tops are subject to extreme cold due to elevational effects, while populations in valleys are equally limited by the pooling of cold air in valley bottoms; only on mid-slopes is the environment moderate enough for populations to attain very high densities (Tenow & Bylund 1989). Although populations of this insect are temporally regulated by lagged effects of parasitism (Bylund 1995), the climate is sufficiently harsh that topographically differentiated meteorological perturbations lead to microclimatically defined population boundaries that take the form of an elevational gradient (Tenow & Nilssen 1990).

The autumnal moth scenario shares many similarities with Wellington's (1964) qualitative model of population dynamics of western tent caterpillar (*Malacosoma californicum pluviale*) and it may also apply to forest tent caterpillar (Cooke & Roland 2000) because there are similar reports of elevational gradients in forest tent caterpillar egg mortality and defoliation (Gautreau 1964) and latitudinal gradients in outbreak severity (Daniel & Myers 1995).

The first objective of this paper is to present original field data from a recent outbreak, near Cooking Lake, Alberta, which show that egg mortality in winter varies temporally, as a function of both density and temperature, and spatially, as a function of topography and microclimate. A second objective is to summarize: (1) published field data, which show that the vertical distribution of fifth stage larvae is density-dependent: foraging on understorey shrub species is more common at high population densities (Batzer *et. al.* 1995); and (2) unpublished experimental data showing that larval host-plant diet influences adult cold tolerance (Dr. J.R. Spence, unpublished data). The third objective is to consider these results collectively in order to advance the hypothesis that forest tent caterpillar populations are regulated jointly by density-dependent factors (both top-down and bottom-up) and density-independent perturbations. The fourth objective is to outline the implications and the broad relevance of this hypothesis.

The paper is structured as follows. The results section of this paper focuses strictly on observed spatiotemporal patterns of winter mortality and attempts to explain them. In the first part of the discussion, these findings are put into a broader context in order to develop the hypothesis that forest tent caterpillar winter egg mortality is partly determined by winter temperature, and partly by population density, through behavioural and physiological processes that influence vulnerability and susceptibility to winter cold. In the second part of the discussion, a qualitative model is developed which shows how winter temperature acts as both a lateral and a non-linear perturbation (*sensu* Royama 1996b) on forest tent caterpillar survival, and could be an important factor affecting host-parasitoid population dynamics. Finally, because the non-linear perturbation paradigm has broad implications for ecological research, particularly regarding animals living in harsh and variable environments, its importance to conceptual and analytical models is outlined briefly.

8.2 Methods

8.2.1 Study area

The 360 km^2 study area, comprising an irregular grid of 83 plots, was located in the aspen forests around the Cooking Lake-Ministik Hills area, near Edmonton, Alberta (Fig. 8.1). The dominant landform was a rolling terrain overlain by a morainal deposit with knob-and-kettle topography that included numerous lakes of all sizes. Elevation varied from 2300 to 2600 m with the lowest elevations occurring around Cooking Lake and Hastings Lake, on the north part of the grid, the Ministik Lakes on the western end of the grid, and Katchemut Creek on the eastern end of the grid. Locally, the landscape is mostly forested aspen parkland with balsam poplar occurring on wetter, low-lying sites. Regionally, the study area is embedded in a matrix of fragmented aspen parkland dominated by agriculture and cattle ranching.

8.2.2 Winter egg mortality

In early April 1996, forest tent caterpillar egg masses were collected from across the study area. These living egg masses, which were laid in the summer of 1995, were taken from shrubs and trees less than 2m in height and stored in a shelter outdoors. A second sample was collected two weeks later and processed in the same manner. Eggs were allowed to hatch naturally. Unhatched eggs from both samples were individually dissected to determine the various causes of failure and to calculate hatching success.

During the summer of 1997 the canopies of those same stands were re-sampled to obtain old egg masses. Little effort was required to sample tree-tops because strong El Niño conditions throughout the spring of 1997 led to an early aspen budburst in northcentral Alberta and a late, wet snow fell on 21 May 1997, weeks after aspen buds had developed into leaves, causing many stems to bend and break under the heavy load. A total of 4528 forest tent caterpillar egg masses were collected from 609 tree-tops and large branches from damaged aspen stems. These old egg masses included cohorts laid in the summer of 1996 and years previous because old egg masses persist for several years on twigs whose radial growth has ceased due to severe defoliation.

When old egg masses were visually compared in the lab, groups could be distinguished on the basis of the nature and degree of: (1) weathering of the spumaline covering the egg mass, (2) erosion around the edges of individual shells of hatched eggs, and (3) fungal development. Using these criteria, each egg mass was assigned a likely cohort year, from 1992 to 1996, old egg masses being more weathered. Classification accuracy was not validated because the final results were not sensitive to errors in cohort assignment.

A sub-sample of old egg masses with unhatched eggs was dissected under a microscope to check for the presence of pharate tent caterpillar larvae to determine the proportion which were either infertile or parasitized. Eggs which failed due to factors other than infertility and parasitism had a blackish appearance due to the head capsules of the pharate larvae showing through the translucent egg shell. This macroscopic feature was found to be a reliable indicator of winter-kill. Consequently, each egg mass was grossly categorized as having either greater or less than half of its eggs winter-killed. This method is much faster than counting eggs individually, and it is almost as accurate for large samples because of the bimodal distribution of egg hatch success during a year of high winter mortality (Witter & Kulman 1972).

8.2.3 Environmental data

Daily minimum temperatures for Edmonton Municipal Airport (113.52°W, 53.57°N) and Edmonton International Airport (113.58°W, 53.30°N) were obtained for the periods 1967-1998 and 1995-1996 respectively. The municipal airport is located 30 km northwest of the study area, within the heat island of the Edmonton urban core and the international airport is situated rurally, 30 km west of the study area, outside the urban heat island (Hage 1972). Elevations for each sample plot on the study grid were obtained by choosing the nearest 25m contour line or elevational landmark shown on 1:50 000 National Topographic Survey maps for Cooking Lake-Tofield. Estimates of forest tent caterpillar cocoon density had been obtained for each stand over the years 1993-1998. The detailed methods of population sampling are described in a related study (Roland & Taylor 1997) on the same grid.

8.2.4 Statistical analysis

Analysis of variance was used to determine if winter egg mortality differed significantly among cohort years. Linear regression was used to determine the effect of altitude and vegetational stratum on spatial variation in winter mortality of the 1995 cohort. For each vegetational stratum, logistic regression was used to describe the dependency of mortality on elevation and density. Correlograms were calculated for model residuals in order to detect any spatial dependence in egg mortality that might implicate the action of other spatially structured processes. All analyses were performed with the R statistical package, version 1.2.1 (Ihaka & Gentleman 1996, Hornik 2001).

8.3 Results

The only cohort year in which winter egg mortality in the canopy was significantly greater than zero was 1995 ($F = 22.3$, $p < 0.0001$). On those egg masses that exhibited partial hatch, the unhatched eggs were often clustered together along the length of one side of the egg mass. Neither the spatial pattern of hatch nor twig orientation was formally recorded in the grid-wide samples. However, an independent sub-sample of 50 egg masses from one stand just south of Hastings L. confirmed that, for egg masses on twigs oriented horizontally, hatch rates were greater for eggs on the top side of the twig. No clustering was observed for egg masses on twigs oriented vertically.

The spatial pattern of winter mortality from grid-wide canopy- and shrub-layer samples was saddle-shaped, with high mortality in the north and south and low mortality in the east and west (Fig. 8.2). Mortality was generally higher at lower elevations, although this relationship might have been exaggerated by a single large patch of low mortality on some high land just south and east of Hastings Lake (Fig. 8.1). Linear regression showed that 49% of the variation in winter mortality of the 1995 cohort could be attributed to the vegetational stratum sampled (70% mortality in shrubs, 25% mortality in canopy; $t = 11.3$, $p < 0.0001$) and altitude (19% higher mortality for each 100m drop in elevation; $t = -4.2$, $p < 0.0001$). When canopy mortality was computed using all cohort-years, the proportion of explained variation remained high, at 66%, suggesting the analysis was insensitive to possible cohort classification errors.

Logistic regression showed that spatial variation in density had no effect on shrub- or canopy-layer mortality. The relationship between winter egg mortality and altitude was significant, although one data point had a strong influence on the regression (Fig. 8.3). This one plot, located near Katchemut Creek on the eastern end of the grid at 2350 m elevation, appeared to be an outlier due to high survival in the canopy and relatively high survival in the shrub layer. The landform here is not knob-and-kettle morainal deposit, but a flat plain that gradually drops in elevation eastward to Beaverhill Lake.

Correlogram analysis of residuals from the logistic regression indicated significant large-scale spatial dependence in egg hatch (Fig. 8.4) which could have resulted from the pattern of cold air drainage occurring after thermal inversion breakdown. Vertical windshear can cause local breakdown of a stable thermal inversion and can result in surface-level patchiness in night-time air temperature (Hage 1972). If a breakdown occurred on the western portion of the grid and cold air drained south and east, this might explain why shrub-layer mortality was high in the southeast while canopy-layer mortality was low. Patterns of mortality caused by thermal inversion breakdown might have been so strong as to dominate any weak patterns of spatially density-dependent mortality.

There were approximately eight cold periods lasting more than two days during the interval from 1 November 1995 to 30 April 1996 (Fig. 8.5). On 18-19 January 1996 rural temperatures dropped several degrees below -41°C, which is commonly cited as the mid-winter cold tolerance threshold of forest tent caterpillar eggs (Hanec 1966). The cold tolerance threshold, however, changes with the seasonal biology of the insect (Hanec 1966), so it possible that anomalously cold weather on 7 March or 24 March might have killed these eggs. Notably, January temperatures within the urban heat island of Edmonton did not drop below -41°C (Fig. 8.5).

Egg mass counts suggested that populations increased steadily from 1992 to 1995 and then declined in 1996 (Fig. 8.6). However, these estimates of egg population densities are biased, and the bias probably increases with cohort age because old egg masses have a greater probability of falling off twigs than recently laid egg masses. Therefore the increase in densities from 1992 to 1995 was probably not as dramatic as egg mass counts suggest, and the drop in density from 1995 to 1996 was probably larger. This is supported by cocoon counts (Roland & Taylor 1997) and aerial defoliation mapping (J. Roland, unpublished data), which suggest that population densities changed little between 1994 and 1995.

A statistical test of association between egg survivorship and population density through time should reveal a density-dependent relationship; however, there are only five temporal observations. Moreover, these are confounded by temporal variation in minimum winter temperatures, which happened to be lowest in the year of highest density (Fig. 8.6). Thus it is unclear from these limited data whether winter egg mortality is related to density.

8.4 Discussion

8.4.1 Winter egg mortality

Cold winter temperatures in January 1996 killed 25% of the 1995 cohort residing in the canopy and 70% of eggs residing in the shrub layer. The population-level mortality rate was probably in between these values and closer to 25%, as most eggs occur in the canopy (Batzer *et. al.* 1995). The reason for clustered patterns of hatch within egg masses is not known. Given that minimum temperatures were above freezing on January 11, and that heavy snow fell on January 15 and 16, it may have to do with an excess of moisture clinging to the underside of the egg mass prior to the deep freeze, an effect that could be exacerbated by the hygroscopic nature of spumaline (Hodson & Weinman 1945)

The vertical differences in mortality within and between plots suggest that frost-pooling was likely a contributing factor to the geographic pattern of hatch. When elevations differ by hundreds of metres, temperatures are typically cooler at higher altitudes; however, when elevations differ by only tens of metres, spatial patterning of temperature is largely determined by patterns of cold air drainage over the topographical landscape, especially during still nights under stable thermal inversions. Therefore high mortality at low elevations was probably a result of cold air draining from high ground and pooling in sloughs and ponds. Cold air perhaps did not pool at Katchemut Creek, but drained off the plain through the creek valley. This would explain anomalously good egg survival at this lowest elevation. Local frost pooling may be especially common on the moraine because of the knob-and-kettle topography. Of course, regression models indicating a strong relationship between altitude and mortality should be viewed with some scepticism because large-scale gradients in mortality and elevation imply that the experimental design was pseudoreplicated (Hurlbert 1984). If residuals from a regression model are spatially autocorrelated, this violates the independence assumption, and reported significance levels may be severely overestimated (Legendre 1993).

Temporal variation in the effect of temperature on mean egg survival can not be entirely due to differences in population density because population densities were just as high in 1993 as they were in 1995 yet egg mortality was much higher in 1995 (Fig. 8.6). Although possible, it seems unlikely that such a large difference in mortality could be due to observed differences in minimum temperature. The low daily minimum of -37.8°C observed in January 1996 was only a little colder than the low daily minimum of -36.5°C observed in February 1994 (Fig. 8.6). One possibility is that the actual on-site temperature difference might have been larger than these urban measurements indicate. Alternatively, winter-kill may be influenced not only by the acute effect of low daily temperatures, but also by the degree of physiological preconditioning before exposure to abnormal cold and by the length of exposure. These effects, which are not captured in a single physical parameter such as a daily minimum temperature, could vary considerably between years.

Another possibility is that, after natural selection by a cold-weather anomaly, the surviving population might be more cold-tolerant (lower susceptibility) or cold-avoidant (lower vulnerability) than the original population. This would have an obvious influence on the predicted dynamics and could further explain why hatch rates for the 1995 cohort were low in 1996 but were not low for the 1996 cohort in 1997 (Fig. 8.6).

8.4.2 Winter weather patterns

The patterns of daily minimum temperatures during the winters of 1992-1993, 1993-1994, 1994-1995, 1995-1996 differed significantly in terms of likely preconditioning and exposure effects (Fig. 8.7). For example, the winter of 1995-1996 exhibited particularly strong phasing of warm and cold episodes which might have led to unfavourable conditions for egg survival on all three counts: premature physiological changes, acute cold, and prolonged exposure. The coldest temperature of -37.8°C occurred 8 days after the minimum temperature had reached +4.1°C during a warm spell, and for 14 days thereafter the minimum did not exceed -24.0°C. Under these conditions, it may be that pharate larvae, before being subjected to extreme and prolonged cold, underwent physiological changes in cold tolerance normally associated with spring time (Hanec 1966). Or perhaps the snow that fell on January 15 and 16 moistened the egg mass coating sufficiently to facilitate freezing.

In contrast, although the minimum daily temperature during the winter of 1993-1994 was nearly as cold, the highest minimum during the previous warm phase was only −4.1°C, occurring 9 days earlier, and temperatures rebounded upward immediately afterward, such that any exposure effect might be minimal. Daily fluctuations during the winters of 1993-1993 and 1994-1995 did not indicate a rapid drop from extreme warm to extreme cold followed by prolonged cold, suggesting that preconditioning effects, acute effects, and exposure effects during those years also probably favoured good survival.

Cold surges, a common feature of Albertan weather, especially in mid-winter, occur when Arctic air intrudes from the northeast and is blocked by the Rocky Mountains (Colle & Mass 1995). As a result, temperatures typically drop by 20-30°C while a high-pressure ridge develops along the eastern slopes, frequently in association with a low pressure trough along the western slopes. The meridional flow that develops along the western slopes tends to divert warm, moist Pacific air away from Alberta and toward the American Pacific Northwest (Changnon *et. al.* 1993). Due to the frequency of these cold Arctic anomalies in winter, forest tent caterpillar populations in Alberta may be particularly vulnerable to winter-kill.

The risk of winter-kill may be further heightened by the fact that these so-called "cold-air outbreaks" sometimes occur shortly following intrusions of warm, moist maritime air originating from the American Pacific Northwest (Hartjenstein & Bleck 1991). Indeed this was the case with the January 1996 Arctic anomaly. Here, rapid, large-scale shifts in jet stream flow were associated with sudden transitions between extreme warm and extreme cold over central Alberta (Fig. 8.8). On January 11 warm air was drawn northward up the eastern slopes of the Rocky Mountains in association with a meridional pattern of jet stream flow. That moist air cooled January 12 and the jet stream shifted to a southern position, establishing a zonal flow pattern on January 13. A second, smaller meridional blocking pattern began developing on January 14 in association with the freshly cooled, moist air. The jet stream rippled on January 15, bringing in additional moisture from the Pacific, and the meridional block climaxed January 16, bringing snow to the Edmonton area on both days. The blocking pattern degenerated on January 17 as the jet stream shifted toward a deep southern trajectory. On January 18 extremely cold Arctic air moved in from the north, and persisted for several days. The net change in temperature over that time was more than -42°C.

Such anomalies, while infrequent, are not rare in Alberta. Another cold-air outbreak in February 1989 was carefully documented by Hartjenstein & Bleck (1991). Daily minimum temperatures here followed a pattern remarkably similar to the January 1996 sequence, as did the pattern of daily snowfall (Fig. 8.7). The example is particularly noteworthy because, like the January 1996 perturbation that assisted in the collapse of the 1992-1995 tent caterpillar outbreak, the sudden change from Pacific to Arctic weather in February 1989 may have assisted in the collapse of the 1987-1988 tent caterpillar outbreak that occurred across central Alberta (chapter three).

Although sudden flips between extreme Pacific and Arctic anomalies might occur only once every few winters, milder transition sequences seem to be a normal feature of Rocky Mountain-induced atmospheric cyclogenesis (Keshishian *et. al.* 1994, Davis 1997). In particular, western Alberta, being that much closer to the eastern slopes of the Rocky Mountains, may be more prone to lee cyclogenetic effects (Bannon 1992).

If tent caterpillars in western Alberta are more vulnerable to preconditioning by Pacific winter anomalies, this might explain why outbreak dynamics seem less globally stable in southwestern Alberta than in colder northeastern Alberta (chapter five). This would also be consistent with the conjecture that: (1) localized outbreaks around Edmonton in 1938 and 1946 stalled temporarily as a result of daily minimum temperatures of -46°C and -43°C occurring on February 8, 1939 and February 1, 1947, respectively, and (2) subsequent outbreaks in 1942 and 1949 were related resurgences that also happened to collapse prematurely as a result of daily minimum temperatures of -44°C occurring both on January 20, 1943 and January 14, 1950, respectively. A more rigorous study of such associations is therefore essential. It would be particularly enlightening to test whether sub-decadal spatial exclusion of local outbreaks (chapter six) could result from partially density-dependent perturbation effects of winter temperature.

It is not clear whether mortality in 1996 was due solely to a drop from high to low temperatures, or if snowfall played a role as well. It may be that warm weather did not alter egg physiology, but only served to enhance the moisture-holding capacity of the outer spumaline, making eggs more vulnerable to freezing. The February 1989 cold snap was also preceded by heavy snow. On the other hand, all mid-winter cold-air outbreaks seem to be preceded by snow (Fig. 8.7).

8.4.3 Density-dependent vulnerability and susceptibility to cold

With regard to the spatial and temporal patterns of winter mortality, there are two reasons to suspect that these eggs were predisposed to winter-kill through density effects. First, high egg mortality occurred only after populations had been at epidemic levels for several years, from 1993 through 1995. With so few observations, this may be mere coincidence. However, similar observations have been made with surprising regularity (Prentice 1954, Gautreau 1964, Witter & Kulman 1972), suggesting the association between winter mortality and density may be more than coincidental. Second, it seems unlikely that temperature variation alone could produce patches and gradients of 0% to 100% mortality among plots.

There are two good mechanistic reasons to suspect that winter temperature acts as a partially density-dependent perturbation on egg survival. First, the vertical distribution of egg masses is density-dependent, and this influences winter cold vulnerability. To see why this is so, consider: although moths prefer to oviposit in upper branches of the tree crown, and especially on the terminal shoot (Batzer *et. al.* 1995), they will oviposit in low trees and shrubbery at extremely high densities, as observed in this study. Due to cold-air pooling, egg masses laid in shrubbery are more vulnerable to perturbation by winter cold. Because the effects of winter temperature depend jointly on the availability of a fixed resource, it acts as a lateral perturbation on egg survival (Royama 1996b).

Second, the quality of foliage consumed by larvae is density-dependent (Batzer *et. al.* 1995), and the quality of larval diet influences cold hardiness of eggs in the following generation (Dr. J.R. Spence, unpublished data). Again, some explanation is required.

Large larvae will consume the foliage of non-host tree species, such as balsam poplar (*Populus balsamifera*), willow (*Salix* spp.) and birch (*Betula papyrifera*), if aspen foliage is in short supply (Nicol *et. al.* 1997). When densities are extremely high and aspen are completely defoliated many fourth and fifth stage larvae are forced to forage on understorey shrub species, such as hazel (*Corylus cornuta*), saskatoon (*Amelanchier* spp.), alder (*Alnus* spp.) and even wild rose (*Rosa* spp.) (Batzer *et. al.* 1995). Hence the claim that the vertical distribution of large larvae is density-dependent. Experiments show that larvae fed a diet of these non-host species during the fourth and fifth larval stage produce eggs that have significantly lower overwintering survival rates compared to larvae reared on aspen (Dr. J.R. Spence, unpublished data). The mechanism by which larval host-plant diet affects cold tolerance in progeny is unknown, but the ill effects of non-host consumption are compounded with the proportion of time spent foraging on non-hosts (Nicol *et. al.* 1997). Because the effect of winter temperature on egg mortality may be very weak at low densities and very strong at high densities, winter temperature constitutes a non-linear perturbation effect (Royama 1996b).

Similar non-linear perturbation effects could also arise through herbivory-induced defenses in the principal host species. For example, if populations at high densities have no choice but to feed on aspen whose defenses have been activated by previous defoliation, they may experience sub-lethal physiological effects that make them more susceptible to extreme winter cold. This possibility has not yet been investigated, but it is known that there are genes in hybrid poplar whose expression is induced specifically by forest tent caterpillar herbivory (Dr. Peter Constabel, personal communication).

8.4.4 Relevance to tent caterpillar dynamics

The perturbing effect of winter temperature can best be understood by modeling the independent effects of temperature on egg survival and population density on susceptibility and vulnerability to winter cold. Five data points are far too few to parameterize a non-linear surface; however a set of three conditional survival curves fit by eye can serve to illustrate the independent components of the perturbing mechanism

(Fig. 8.9). Expected egg survival should follow a sigmoid dose-response to temperature, where LT_{50} defines the daily minimum temperature required to kill 50% of a population, and observed egg survival rates should depart from this curve in proportion with changes in state variables such as density, or parameters such as genetic constitution (Fig. 8.98a). Vulnerability to winter-kill should be non-linearly density-dependent as a result of competition for oviposition sites in the upper canopy, but because competition is for a fixed resource, this curve should shift laterally according to fluctuations in temperature (Fig. 8.9b). Susceptibility to winter-kill should also be non-linearly density-dependent for cold temperatures but should be insensitive to changes in density for warm temperatures (Fig. 8.9c). According to this perturbation model, then, the expected egg survival rate for a given low temperature is dictated by the curve in Fig. 8.9a, and then dynamic adjustments for density-dependent vulnerability and susceptibility are given by the curves of Fig. 8.9b and Fig. 8.9c. If winter temperature is a normally distributed random variable, then the realized egg survival rate is determined jointly by randomly sliding along the curve in Fig. 8.9a and bouncing between the sets of curves in Figs. 8.9a and Fig. 8.9b. Thus temperature acts as both a lateral and non-linear perturbation on egg survival (Royama 1996b).

If the normal minimum winter temperature is equivalent to the temperature required to freeze 50% of eggs (LT_{50}), then expected survival would be a normally distributed random variable. If, instead, eggs are well adapted to winter cold, then, by definition, the normal minimum winter temperature would be higher than the temperature required to freeze 50% of eggs (LT_{50}). Here, the perturbation effect will have a skewed distribution such as a gamma distribution.

The effect of stochastic, gamma-distributed, partially density-dependent winter egg survival on a population's dynamic will depend strongly on how the deterministic dynamics are specified. In general, a perturbation acting this way will have a stronger destabilizing effect than a normally distributed, density-independent, vertical perturbation. For example, in an oscillatory host-parasitoid interaction, a strong perturbation may have a weak effect if it occurs at low host-density and a weak perturbation may have a strong effect if it occurs at high host-density - the degree of asymmetry here depending on the degree of non-linearity in density-dependence. The result is that population oscillations are more erratic. This is important because it suggests theoretical results based on normally distributed, density-independent, vertical perturbation effects (*e.g.* Royama 1996b) may be irrelevant for some systems. Although a comprehensive analysis is beyond the scope of this chapter, the topic is explored in some depth in chapter eight.

If winter mortality is partially density-dependent, this might explain why statistical evidence of an association between winter temperature and egg survival (Witter & Kulman 1972) and generational survival (Daniel & Myers 1995) is so elusive in temporal analyses, yet so clear in spatial analyses (Roland *et. al.* 1998, Cooke & Roland 2000). It might also explain why populations sometimes survive temperatures colder than -43°C (Gorham 1922): low-density populations might be more cold tolerant than Hanec (1966) showed. Finally, it might also explain why winter egg mortality exhibits the sort of fine-scaled spatial variation shown in this study and others (*e.g.* Witter & Kulman 1972).

If the understorey and the canopy are very different worlds with regard to a caterpillar's vulnerability and susceptibility to winter mortality, then density-dependence of perturbation effects might be highly non-linear. In other words, given a certain winter minimum temperature, densities might have to surpass some upper threshold before the understorey effects play a major role in precipitating population collapse. Under normal winter temperatures, very high densities would be required for perturbation effects to occur; under very cold winter temperatures, perturbation effects would occur regardless of density.

If the understorey is indeed such an unfavourable environment, then why would any moth choose to oviposit there? And why would populations in both the understorey and canopy collapse after perturbation? Why wouldn't canopy populations persist? These questions merit some consideration.

First, the cost of ovipositing in the shrub layer might not be as costly as one might first presume. For moths that emerge early, the best oviposition sites in the canopy are available for occupation. But for moths that emerge late, canopy oviposition may entail a tangible loss in fitness in terms of food competition, parasitism risk, and disease transmission rates among progeny. Supposing moths can assess local densities, ovipositing in the shrub layer may be a "poor man's strategy" of making the best of a bad situation: accept the risk of winter mortality in exchange for reduced larval crowding in the following spring. Indeed, this might explain why forest tent caterpillars generally are such early feeders: there may be strong selection for individuals that can secure access to food, whether through ovipositing in ideal locations that are unoccupied, or ovipositing elsewhere when ideal sites are occupied, or hatching early in the spring to beat out competitors. The view is compatible with the observation that fourth and fifth instars readily abandon the gregarious feeding behaviour of earlier stages, preferring to feed individually. It would also explain why larvae routinely risk the climatic perils of early hatch (*e.g.* Blais *et. al.* 1955) but not the nutritional perils of hatching so early that buds are not available for forage (Parry *et. al.* 1998). Notably, the risk of mortality due to cold spring weather suggests that forest tent caterpillars may be "between a rock and a hard place" in terms of further optimizing a phenological strategy for minimal impact of cold winter and spring weather.

As for the lack of persistence of canopy populations following perturbation, it is suspected that the lagged interaction between hosts and mobile Dipteran parasitoids is responsible. Suppose that parasitoid populations increase as long as host populations are increasing. Once the host population expands into the shrub layer, this sub-population becomes more vulnerable and more susceptible to perturbation. Yet both host and parasitoid populations continue to grow as long as a perturbation does not arrive. The arrival of a sufficiently large perturbation might take a year or two or more, depending on local climatic means and the particular phasing of low-frequency climatic fluctuations. The longer the lag between the onset of shrub-layer occupancy and perturbation arrival, the higher the parasitoid:host ratio builds, and the more "brittle" the host-parasitoid community becomes. With the arrival of a winter climatic perturbation, shrub-layer and frost-pool occupants may die, but because parasitoids are in the soil, they survive. Therefore the ratio of parasitoids to hosts is extremely high and the collapse of canopy populations during that summer is inevitable. In this scenario, were it not for the delayed density-dependence of parasitism, canopy populations might persist in spite of perturbation.

8.4.5 Relevance to other systems

Moilanen & Hanski (1998) mention that "one potentially significant mechanism affecting population turnover is interaction between habitat quality and climatic perturbations", and they describe how this could apply to butterflies foraging in meadows. However they do not go the extra step of generalizing the mechanism or considering the implications for the dynamics of a predator-prey interaction.

This study is among the first to document clearly non-linear perturbation effects. A few studies have considered the importance of interactions between sub-lethal and lethal processes, such as the effect of parasitism on predation (Roland 1990, Murray *et. al.* 1997, Ives & Murray 1997). Others have described situations where populations compete for a density-independent resource. Examples include grasshoppers competing for shade (Uvarov 1931) and titmice competing for nesting holes (Royama 1996b).

When a limiting resource fluctuates, it acts as a lateral perturbation on population dynamics (Royama 1996b). A good example is case of woodpeckers competing for highly variable acorn crops (Hannon *et. al.* 1987). Textbook anecdotes of this variety are numerous, yet few systems have been studied well enough to illustrate the lateral perturbation effect of a limiting resource that fluctuates. Although there are many systems where predisposition to death is partially density-dependent and the proximate cause of death is stochastic and density-independent, the forest tent caterpillar is one of the unusual cases where the partially density-dependent effects of density-independent perturbations are highly non-linear.

Partially density-dependent perturbation effects are likely to arise through interactions between fluctuating, density-independent environmental factors and density-dependent behavioural and physiological processes. For example, where climatic conditions vary tremendously, these can act as a perturbation on survival. But variation in perturbation vulnerability may result from density-dependent spacing behaviour, such as territoriality. Similarly, variation in perturbation susceptibility may result from density-dependent tolerance thresholds, such as through food competition effects on animal vigour. Clearly, there are a multitude of mechanisms that could potentially interact with density-independent perturbation severity to generate partially density-dependent perturbation effects. These include both top-down and bottom-up forces.

Perturbations that act in a partially density-dependent manner have been described as "lateral" and "non-linear" perturbations, to distinguish them from "vertical" perturbation whose effects are completely independent of density (Royama 1996b). These geometrical epithets refer to the manner in which the density-independent perturbation moves a population trajectory away from a density-dependent attractor (see Fig. 1.6, 1.12, and 1.13 in Royama 1996b). All other things being equal, a factor whose impact is much stronger at high densities than at low densities acts as a non-linear perturbation on survival. Note the importance of distinguishing between the perturbation, which fluctuates independently of density, and its impact, which may be density-dependent.

The types of systems where non-linear perturbation effects are likely to arise include cases where: (1) animals live in harsh and fluctuating environments; (2) population dynamics are characterized by sudden declines; (3) life table analysis has not revealed any one factor to be a key factor; (4) experimentation reveals interactions between biotic and abiotic factors are a common cause of death. This is the case with the forest tent caterpillar and with many other species of forest dwelling insects.

There may be many systems that involve density-independent perturbations whose effects are partly determined by density-dependent physiological parameters. These are the sort of systems Lack (1954) might have had in mind when he contemplated the constancy of bird populations. For example, if individuals in fringe environments are more vulnerable and more susceptible to perturbation-caused mortality, then individuals with territories will tend to persist, leading to a low-variance fluctuation. It is ironic that "floaters" are often ignored in demographic studies, because it is largely their fate that would reveal whether a population is regulated by partially density-dependent perturbation effects.

The ultimate test of whether populations are regulated by partially density-dependent perturbations must come from analysis of detailed surveys under natural conditions. This, however, is not possible with current statistical and methodological approaches to life-table analysis. In addition to the well known statistical problems of detecting density-dependence (Royama 1996a), there is the additional analytical problem of detecting density-independent perturbation effects when the stochastic, density-independent effects are dynamically mixed in with the deterministic, density-dependent effects (Royama 1996b). Even with the most powerful techniques available, this is not possible when the perturbing factor is autocorrelated, asymmetrically distributed, and non-stationary, and when its effects are partially density-dependent. All of these problems are inherent in the data presented here.

The issue of whether population fluctuations are governed by partially density-dependent perturbation effects relates directly to the more general empirical debate of whether tri-trophic herbivorous systems are regulated primarily from the top-down, by factors such as parasitism, predation, and disease (Turchin 1990, Berryman 1996), or from the bottom-up, by factors such as host-plant quality (Larsson 1989, Hunter *et. al.* 1997) and intrinsic quality of the herbivore (Chitty 1967), or from "lateral" effects such as competitive interference and dispersal (Harrison & Cappuccino 1995). A problem with the top-down *versus* bottom-up debate is that different types of factors may regulate populations in qualitatively different ways. For example, density-dependent dispersal, lagged parasitism, and large-scale forest structure may be responsible for high, medium, and low-frequency fluctuations in spruce budworm populations (Royama 1997). Also, interactions among these processes may prevent any one single factor from standing out as a key factor (Harrison & Cappuccino 1995). If populations are frequently regulated by partially density-dependent perturbation effects, this might explain why evidence for either view seems equivocal. Similarly, where survival is jointly determined by density-independent perturbations and density-dependent tolerance to perturbation, population fluctuations may be only vaguely density-dependent (Strong 1986), such that neither the density-dependent nor the density-independent hypothesis is correct. So while these dichotomies help to distinguish the conceptually different types of regulatory processes, they do not offer a useful starting point for understanding particular systems that may be regulated by multiple factors. For this, a general synthetic model may be required.

The principal value of the non-linear perturbation concept lies in its ability to synthesize several disparate classical ideas into a single intuitive framework. For example, "population limitation" is used to refer to both the process by which population numbers in a certain area are prevented from exceeding an upper threshold, and the process by which populations are prevented from spreading into neighbouring areas. By differentiating between vulnerability and susceptibility, the non-linear perturbation concept suggests important distinctions between spatial versus temporal processes and density-independent versus density-dependent processes. According to it, the biological mechanism responsible for temporal limitation may not be the same as the one driving spatial limitation, and either constraint may fluctuate both randomly and as a function of density. The processes that govern population fluctuations are intimately linked with those determining its distribution, and the interaction is especially important for understanding spatiotemporal changes in population boundaries. Thus the non-linear perturbation concept provides a synthetic framework that unifies the seemingly disparate views of Nicholson (1954) and Andrewartha & Birch (1954). Also, by refusing to categorize stochastic environment-organism interactions as purely density-independent or purely density-independent, the non-linear perturbation concept validates and perhaps clarifies the hypothesis of density-vague population fluctuations (Strong 1986) and imperfect density-dependence (Milne 1957, Berryman 1992, Turchin 1995).

When regulation is jointly caused by top-down and bottom-up mechanisms, neither view alone explains the dynamic. When little is known about a particular system, these should not be considered *a priori* mutually exclusive hypotheses. The non-linear perturbation concept accommodates both types of processes, showing how the role of a plant-herbivore relation in a tri-trophic interaction may be rather insidious. Although latent cycles may be induced by delayed density-dependence of parasitism, oscillations might be sustained by random perturbation and their frequency increased by density-dependent perturbation tolerance thresholds. This shows why it is important to move past qualitative questions about what causes cycles to more precise quantitative hypotheses that are based on dynamic modeling (Kendall *et. al.* 1999).

8.4.6 Evolution of perturbation tolerance

One might expect that continual natural selection by a density-independent factor, such as winter cold, should eventually lead to the evolution of perturbation tolerance. The non-linear perturbation model, however, provides a mechanism whereby the regulatory impact of a density-independent factor might persist, in the long-run, despite evolutionary pressures toward increasing tolerance. First, when perturbation impacts depend on interactions with other variables, selective pressures need not be large for a species' dynamics to be dominated by perturbations. Indeed, selection may be sporadic rather than continual. Second, selection may favour behavioural adaptations minimizing vulnerability over physiological adaptations minimizing susceptibility, and these behavioural adaptations may have their own particular fitness costs. In the forest tent caterpillar, for example, oviposition in the forest canopy by moths might be more strongly selected for than physiological cold tolerance of eggs, and this could lead to a competitive race among individual females to occupy prime oviposition sites as soon as possible. Evolutionarily, this could be accomplished in the adult stage by mating as soon as possible after pupal emergence and dispersing as little as necessary, or in the earlier stages by hatching as soon as possible and completing larval development as quickly as possible. Of course, enhanced winter survival may be only one of many benefits of an early phenological strategy. The main point is that non-linear perturbation effects may serve to sustain a certain level of physiological cold tolerance, while constraining the evolution of further increases in physiological cold tolerance. In general, then, the hypothesis that animal population dynamics may be strongly influenced by partially density-dependent perturbation effects is not at all inconsistent with a theory of evolution by natural selection.

8.5 Conclusion

There is excellent evidence that forest tent caterpillar eggs can not tolerate winter temperatures much below a certain threshold and that this tolerance threshold is occasionally exceeded in Canada. There is good evidence that vulnerability of forest tent caterpillar eggs to winter freezing depends on small-scale microtopoclimatic effects, and that susceptibility is in part determined by parental larval host-plant quality. There is some evidence of a preference for canopy oviposition and foraging which can not be fulfilled at very high population densities. Collectively, this suggests winter mortality of eggs may be driven by partially density-dependent perturbation effects. The question is: how non-linearly density-dependent are these effects?

Fine-scaled measurements of temperature through the shrub layer and canopy would help to determine the extent to which spatial patterns of mortality are driven by vertical and horizontal gradients in temperature. Investigation into the mechanism by which parental larval host-plant quality determines cold hardiness of progeny could reveal whether density-dependent cold-tolerance is a result of foraging on non-host-plants or a result of delayed induced response to defoliation within the primary host-plant species. Studies of oviposition and foraging patterns could reveal to what extent these processes are density-dependent or stochastic. For example: do caterpillars choose to forage in the understorey, or are they inadvertently blown there from the canopy by rain and windstorms? Is oviposition in the understorey the result of individual choices made after detecting high densities in the upper canopy, or are understorey-dwellers merely incapable of upward flight? Or, if upward flight is temperature-dependent, is understorey oviposition a result of continuously cold night temperatures? Strong density-dependence in oviposition and foraging would favour the view that winter temperature acts as a highly non-linear perturbation.

The mechanism of perturbation has a strong influence on the possibility of population synchrony through a Moran effect (Moran 1953, Royama 1996b). It is frequently assumed that spatially autocorrelated fluctuations in a perturbing factor implies potential for population synchrony, (*e.g.* Williams & Liebhold 2000b). However, it is actually the spatial correlation structure in the *effect* of the perturbations that determines the strength of the Moran effect. If the effect of a perturbation is partially density-dependent, synchrony may be localized, even if perturbations themselves are regionally spatially autocorrelated.

The effect of extreme cold may be strongly conditioned by temperature-dependent changes in egg physiology prior to exposure, and by the duration of exposure. Experimentation here could be used to develop a temperature-dependent egg mortality hazard index that could be used in a more informed analysis of historical data. Failure to detect a strong effect of a suitable winter temperature hazard index would then favour the possible involvement of partially density-dependent perturbation effects. The issue is important because anecdotes of outbreak collapse in association with cold winters are sporadic, and it is unclear whether this is because of incomplete records, incomplete knowledge of temperature-mortality dose-response relationships, or the involvement of multiple factors.

Non-linear physiological responses to temperature also have a strong influence on the potential for population synchrony through correlated perturbation. The scale of spatial autocorrelation in a perturbation index may be quite different than for the climatic parameter upon which it is based. For example, whereas the temperature field may be highly autocorrelated and gradient-like, the conditional risk of mortality due to cold may be more sharply defined and patchy, and it is this second quantity that determines the potential for population synchrony through a Moran effect.

The qualitative non-linear perturbation model presented here is not offered as a complete description of forest tent caterpillar population dynamics, for there are many important deterministic and stochastic processes not considered. These include disease transmission, predation, and dispersal - each of which may be subject to its own suite of perturbing factors. Inclusion of such effects could eventually lead to a more quantitative and synthetic model capable of generating test-worthy predictions.

The concept of partially density-dependent perturbations is not new, yet the theoretical implications have not been formally considered in the literature. In empirical modeling it is typically assumed that perturbations are density-independent and that their impacts on survival are also density-independent. This simplifying assumption poses two problems. First, if perturbation effects are non-linearly density-dependent rather than purely density-independent, this alters the density-dependent structure of a plant-host-parasitoid interaction and, therefore, the expected population dynamics. Second, it may not be possible to detect such stochastic effects unless density is factored into the analysis, which is not a simple statistical matter.

To be truly useful, a thorough analysis of the statistical properties of theoretical systems governed by non-linear perturbations is required. However, it may be that analytical approaches to the empirical detection of such effects are not possible and that experimentation and process-oriented simulation is the only alternative. This is an open question that should interest ecological statisticians and quantitative ecologists.

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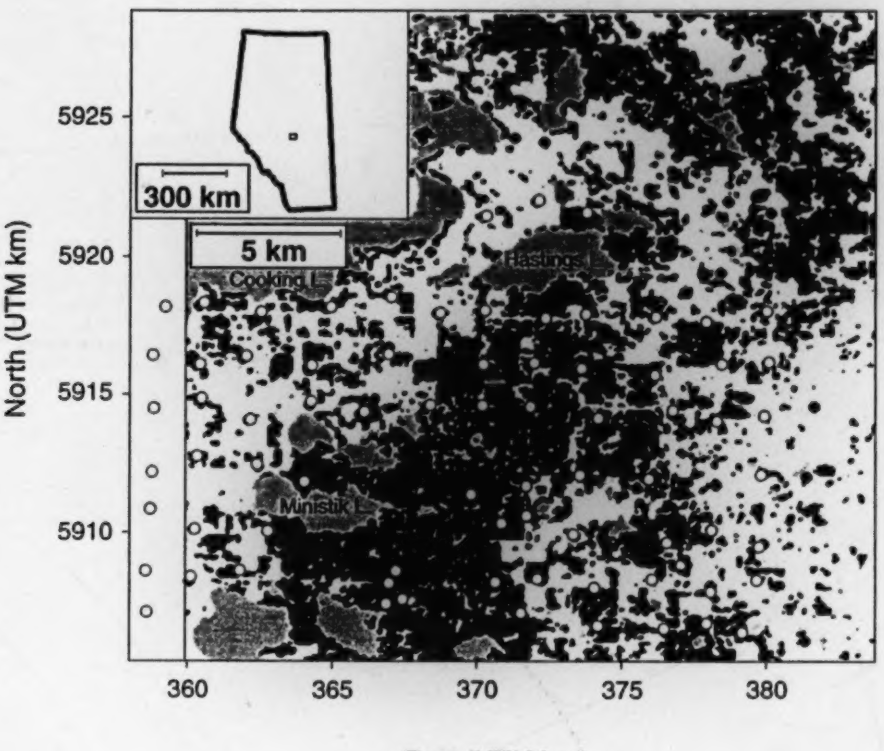
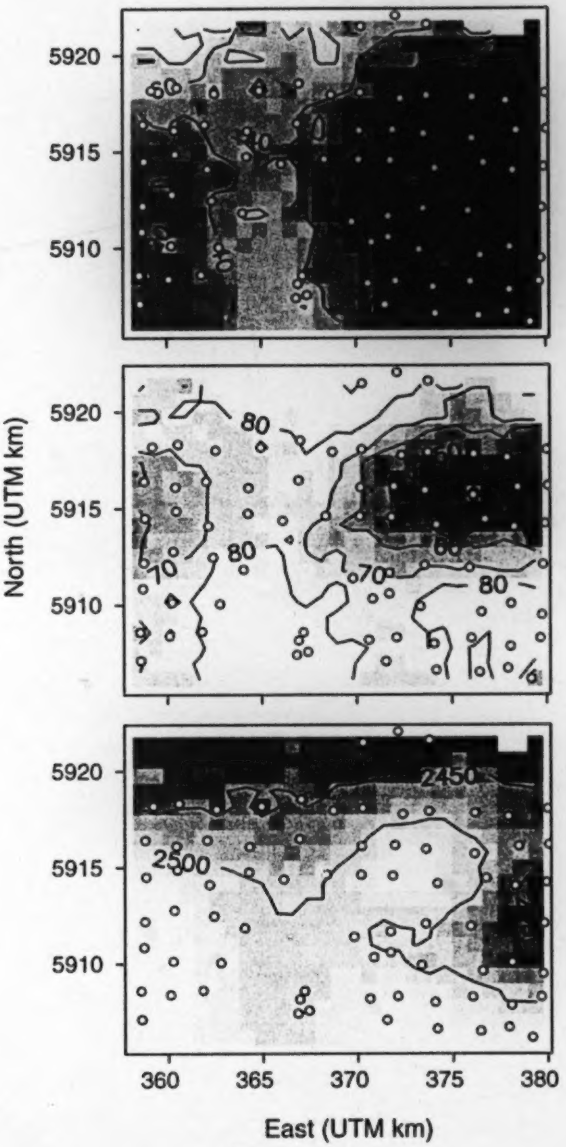

300 km
5 km
Cooking L.
Hastings L.
Ministik L.
North (UTM km)
5925
5920
5915
5910
360
365
370
375
380
East (UTM km)

Figure 8.1. Aspen stands sampled across the study grid, located in the area of Cooking Lake and Ministik Hills of central Alberta (see inset). Plots, shown as circles, are overlaid onto a classified photo-mosaic indicating forest (black), clearing (white), and water (grey).


5920
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North (UTM km)
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East (UTM km)

Figure 8.2. Spatial patterns in percent winter egg mortality in the canopy (top), and shrub layer (middle), compared to elevation (bottom), measured in feet.

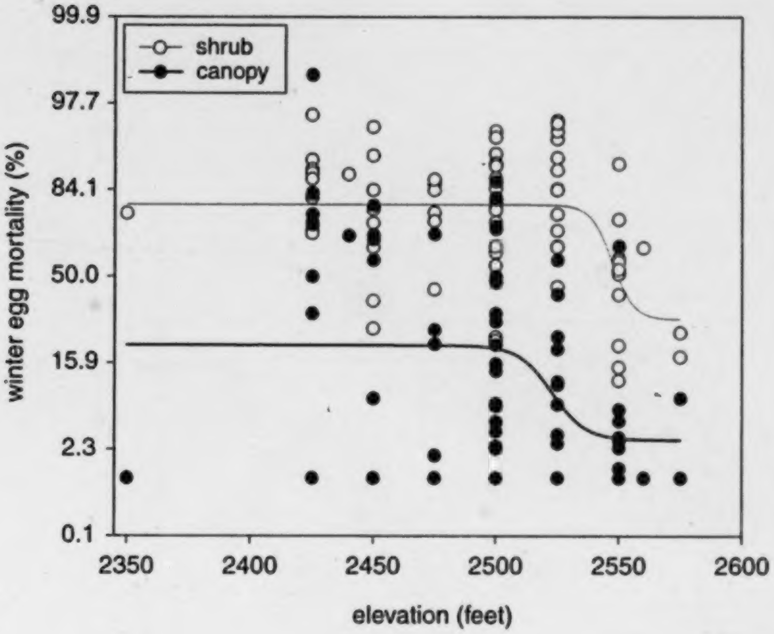

Figure 8.3. Winter egg mortality (probit scale) as a function of elevation and vegetational stratum. Curves for each stratum fit by logistic regression. Note: cocoon densities in 1995 were not significant in logistic regression.

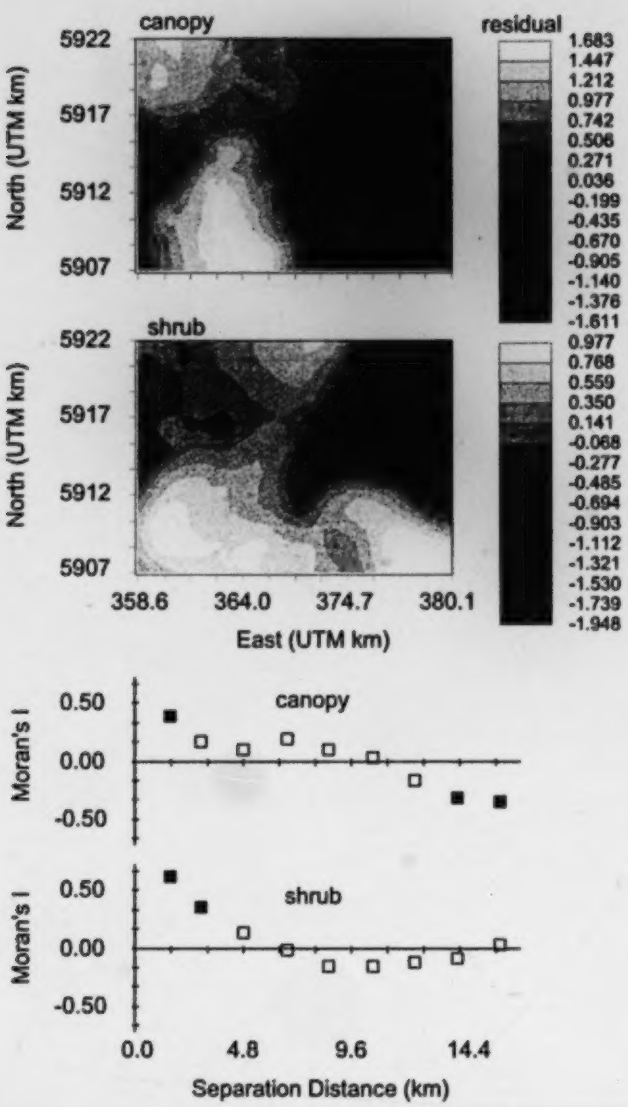

Figure 8.4. Residuals from logistic regression of canopy- and shrub-layer mortality on elevation and 1995 cocoon density across the Cooking L. grid. Bottom correlograms show gradients in residuals. Filled squares denote significant autocorrelation athe the 95% confidence level.

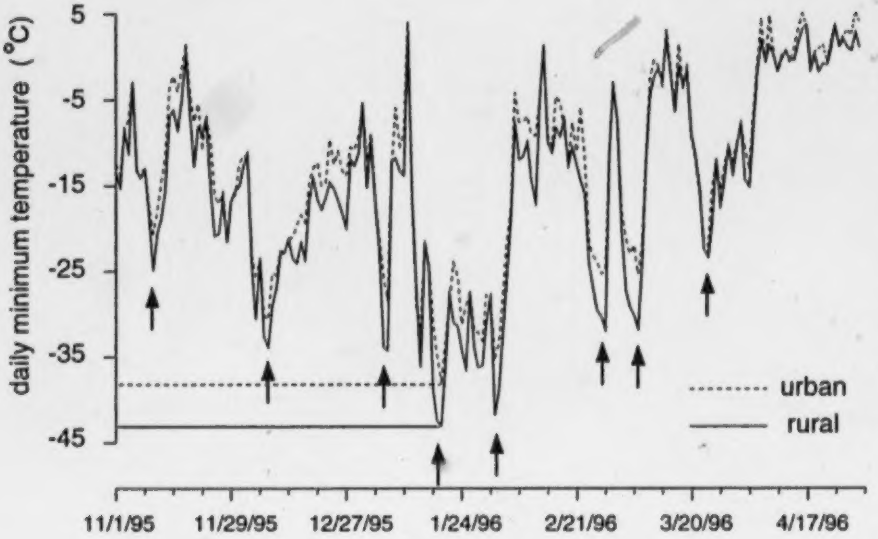

Figure 8.5. Daily minimum temperatures from 1 November 1995 to 30 April 1996 for Edmonton International Airport (rural, solid line) and Edmonton Municipal Airport (urban, dotted line). Arrows indicate prolonged cold events. Horizontal lines indicate winter low temperatures at each location.

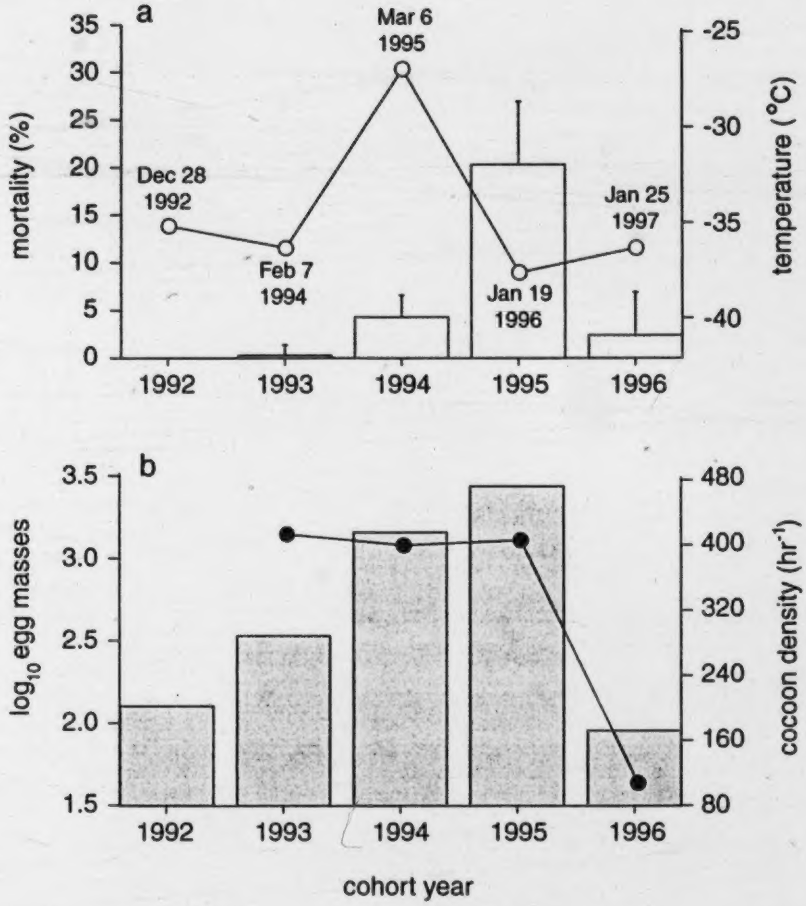

Figure 8.6. (a) winter mortality of canopy-dwelling eggs laid in 1992 through 1996 (bars) and minimum urban temperature recorded each winter (open circles, labelled as to date on which low temperature occurred); (b) number of canopy egg masses assigned to each cohort year (shaded bars) and cocoon density estimates for each cohort year (solid circles).

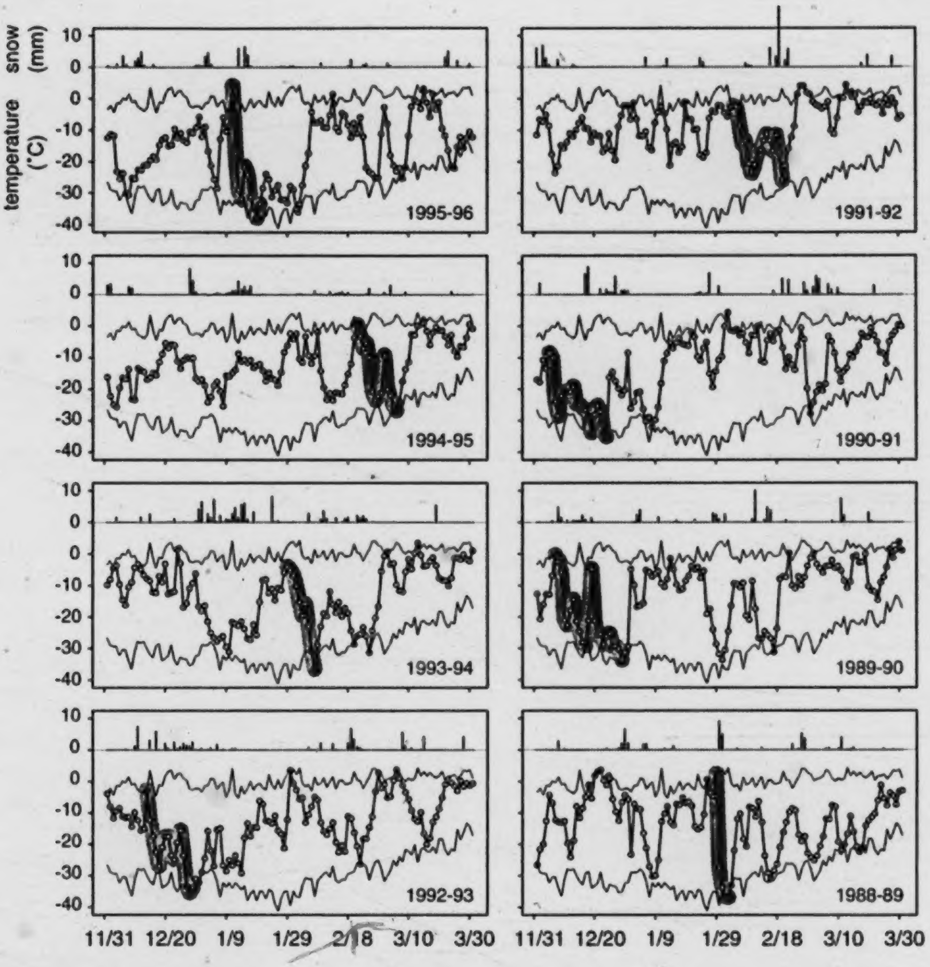

Figure 8.7. Daily minimum urban temperatures (circles) from December 1 to March 31 for the winters of 1988-89 to 1995-96, compared to the long-term extreme high/low daily minimum over the period 1967-1996 (dashed lines). Shaded segments indicate largest and most sudden dips in temperature posing the greatest threat to tent caterpillar eggs. The most severe of these occurred in 1996 and 1989. Only in 1996 did the Arctic anomaly persist. Daily snowfall (bars) shown in upper portion of panel.

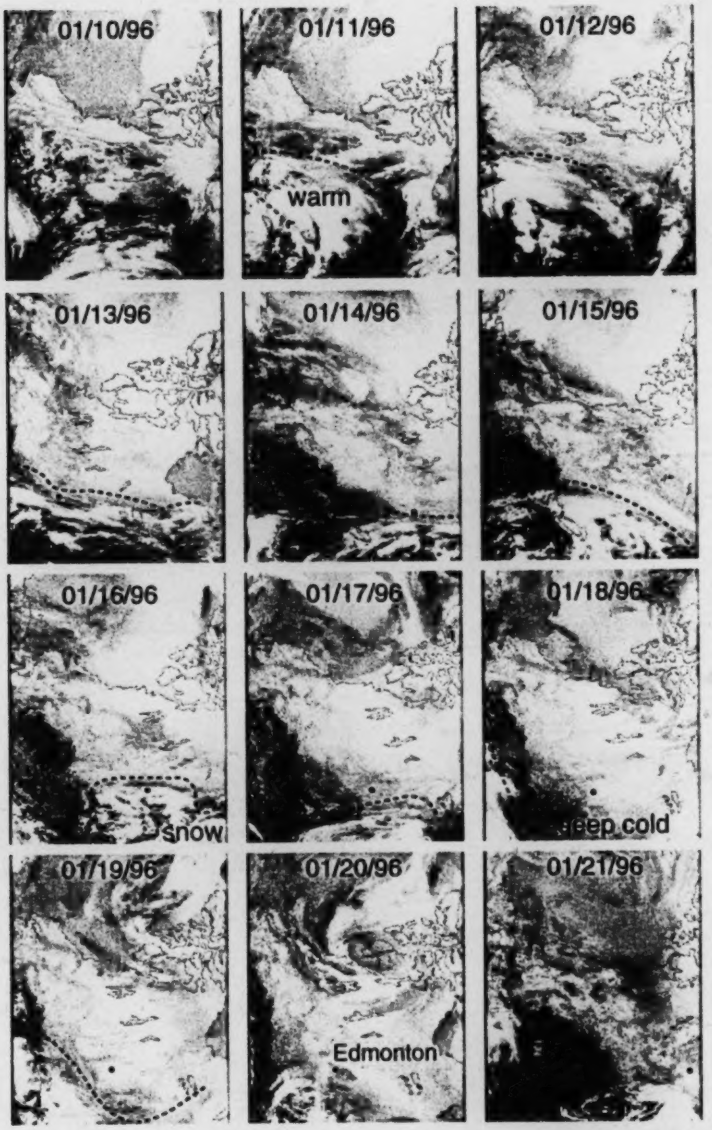
01/10/96
01/11/96
warm
01/12/96
01/13/96
01/14/96
01/15/96
01/16/96
snow
01/17/96
01/18/96
deep cold
01/19/96
01/20/96
Edmonton
01/21/96

Figure 8.8. AVHRR thermal infrared satellite images (courtesy NOAA) of northwestern Canada indicating cloud cover over the period January 10 to January 21, 1996. Dotted line indicates position of jet stream, which flows West to East (left to right).

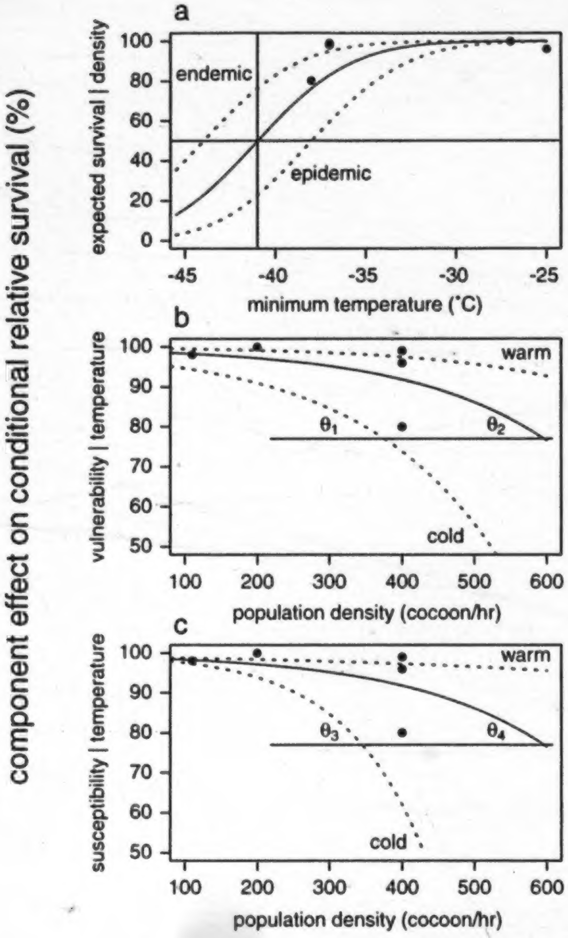

Figure 8.9. Componentry of partially density-dependent perturbation effect of winter temperature on egg survival. Points are time-series data from Fig. 8.6, plotted in phase space. Solid curves indicate conditional effect on relative survival of: (a) temperature; (b) density, through changes in vulnerability; (c) density, through changes in susceptibility. The family of dotted curves represents the effect of the conditioning variable. Horizontal line in (a) represents LT_{50} of -41 °C. Note $\theta_1 = \theta_2$ in (b) implies a lateral perturbation effect and $\theta_3 \neq \theta_4$ in (c) implies a non-linear perturbation effect.

9. ARE FOREST TENT CATERPILLAR OUTBREAK CYCLES INDUCED BY WINTER TEMPERATURE FLUCTUATIONS?

9.1 Introduction

In the aspen parkland region of Alberta, decadal outbreaks of the forest tent caterpillar (FTC) coincide fairly well with decadal cycles in precipitation and solar variability (chapter two). The origin of the correlation is a mystery. Because there is not an obvious mechanism linking these processes, it may be spurious. On the other hand, there could be some direct, biological, causal mechanism by which spring precipitation affects caterpillar population dynamics, such as through effects on host-plant physiology or larval feeding and development, perhaps in combination with predation and parasitism of juvenile larvae (Parry *et. al.* 1998). Alternatively, cycles in precipitation could be associated with cycles in other climatic variables thought to be key factors in caterpillar survival. Outbreaks in northern Alberta are less frequent than in the aspen parkland (chapter three), and this latitudinal gradient in outbreak periodicity could be related to latitudinal variation in climate.

Given that the effect of cold weather on egg hatch is one of the strongest and most universally cited perturbations on caterpillar survival (chapter eight), it was reasoned that, like precipitation, January temperatures might show low-frequency variation and this variation might help explain the occurrence of outbreaks. Specifically, it may be that sub-decadal outbreaks in the aspen parkland in 1913, 1924, 1929, 1937, 1941, 1949, 1957, 1964, 1968, 1976, 1982, 1987, and 1995 were a result of coherent local population cycles whose amplitude was enhanced by autocorrelated stochastic perturbations (Royama 1984) and whose phasing was regionally synchronized *via* a Moran effect (Moran 1953, Royama 1996). Also, given the colder climate of northern Alberta and the greater possibility of continual and severe perturbation, super-decadal outbreaks in the boreal region in 1924, 1942, 1962, 1982 might be a result of low-frequency period-forcing (Ives *et. al.* 2000).

9.2 Methods

9.2.1 Winter temperature data

Estimates of mean monthly temperature for the period 1908-1998 were extracted from the global historical climatological network data set that is regularly maintained by the National Climate Data Centre of the National Ocean and Atmosphere Agency (url: ftp.ncdc.noaa.gov/pub/data/ghcn/v2/v2.prcp.Z). The spatial and temporal extent of data records varied in Alberta. Six weather stations were found to have nearly continuous and complete records (Fig. 3.1): Fort Vermilion (116.0°W, 58.4°N; 1909-1985), Campsie (114.7°W, 54.1°N; 1913-1998), Sion (114.1°W, 53.9°N; 1911-1998), Lacombe (113.7°W, 52.5°N; 1908-1994), Ranfurly (111.6°W, 53.4°N; 1908-1998), and Waseca (109.4°W, 53.1°N; 1908-1998). Elsewhere, gaps in temporal continuity and seasonal completeness were numerous.

9.2.2 Modeling outbreak dynamics

Supposing that minimum daily temperature in January was a key factor affecting winter survival of tent caterpillar eggs, the effect of this variable was incorporated into a spatially implicit predator-prey model simulating large-scale tent caterpillar population dynamics. The model was used to address the following questions:

1. How effectively could the complex interactions among tent caterpillars and their numerous natural enemies be represented by a simple, univariate, second-order, non-linear recruitment process?
2. Supposing that the host-parasitoid interaction leads to slow-damping oscillations of a particular frequency, could winter temperature serve to amplify endogenous cycles (*e.g.* Bulmer 1976, Kaitala *et. al.* 1996), especially given autocorrelated perturbation effects (*e.g.* Royama 1984) caused by low-frequency variability in January monthly mean temperature? Could it act as a phase-locking mechanism (*e.g.* Moran 1953)? Could it acting as a period-forcing mechanism (*e.g.* Ives *et. al.* 2000)?
3. Is there a single density-dependent parameter set that could all allow for

density-independent perturbations to explain both super-decadal cycles in northern Alberta and sub-decadal cycles in southern Alberta? Or are separate density-dependent parameter sets required?

The log-linearized recruitment model took the form:

$$R_t = R_m - \exp(-a_0 - a_1 X_t - a_2 X_{t-1}) + \log_{10} \gamma(\theta_t) \qquad \text{[Eq. 1]}$$

where R_t is the annual generational recruitment rate in year t, which is added to density, X_t, each year, from t = 1906 to 1985, to calculate the new density in year t+1. Capitalization indicates these state variable are $\log_{10}$-transformed. The parameters to be estimated are R_m, the $\log_{10}$-transformed maximum possible recruitment rate, and a_0, a_1, a_2, which govern the equilibrium density and the strength of first-order and second-order feedback respectively.

The dimensionless perturbation function, $\gamma(\theta_t)$, simulates the effect, in year t, of January monthly mean temperature, θ_t, measured in °C, on egg recruitment, and is computed as:

$$\gamma(\theta_t) = \text{normalcdf}(\theta_t; \tau_1, \tau_2) \qquad \text{[Eq. 2]}$$

where τ_1 is the temperature below which more than 50% of a population will die, and τ_2 is a parameter governing the slope of the dose-response relationship.

Given normalcdf(x; μ, σ) is equivalent to:

$$= \int_{y=-\infty}^{x} \frac{1}{\sqrt{2\pi}\sigma} e^{-\frac{(y-\mu)^2}{2\sigma^2}} \qquad \text{[Eq. 3]}$$

this implies $\gamma(\theta_t)$ will follow a gamma distribution for any value of τ_1 that differs from the expected value of the sequence of θ_t. For example, if the normal January monthly mean temperature, $\overline{\theta}_t$, is -20°C, with a standard deviation of 4°C, then a 50% tolerance threshold, τ_1, of -30°C will usually lead to high egg recruitment (*e.g.* $\gamma(\theta_t) > 0.95$) but will occasionally lead to low recruitment (*e.g.* $\gamma(\theta_t) < 0.5$). Note egg recruitment follows a gamma distribution and τ_2 governs the degree of asymmetry of that distribution. The fact that the perturbation effect was asymmetrically distributed implies that it could serve not only as a phase-locking mechanism, but also as a period-forcing mechanism, given sufficient variance (Ives *et. al.* 2000).

Because we were interested in comparing only the autocorrelation structures in outbreak chronologies and simulated caterpillar density, parameters R_m and a_0 were set to their canonical values 1 and 0 respectively. Initial simulations showed that the model's dynamics were insensitive to initial densities X_{1905} and X_{1906}, as long they were not extremely far from equilibrium. These were set to -0.20 and -0.18 respectively. With cold tolerance parameters fixed at $\tau_1 = -30$°C and $\tau_2 = 6$, the endogenous parameters a_1 and a_2 were free to vary.

With respect to January temperature fluctuations, Alberta weather stations could be readily categorized as either northern/boreal (no 6.5-yr cycle) or southern/parkland (with 6.5-yr cycle) (Fig. 8.1). We simulated forest tent caterpillar population dynamics in boreal and parkland Alberta using temperature data from two representative stations. To simulate outbreaks at more than these two locations would have been redundant given the very high coherence in temperature fluctuations among the parkland weather stations. We used actual January monthly mean temperatures from Fort Vermilion ($\overline{\theta}_t = -23.5$°C) and Ranfurly ($\overline{\theta}_t = -16.4$°C) for the period 1907-1985.

Was there one particular parametrization that could mimic, *via* interaction with the cyclic exogenous perturbations, the patterns of asynchrony in the aspen chronologies? In successive simulation experiments, the endogenous parameters were tuned to generate deterministic, damping cycles of frequencies equal to the major frequencies in chronology spectra. Knowing that there were three dominant spectral peaks in aspen chronologies at 10.0, 6.5 and 4.5 years^{-1} (Fig. 3.8), this led to three simulation experiments: ($1+a_1 = \{1.45, 1.05, 0.35\}$, $a_2 = \{-0.80, -0.85, -0.90\}$).

Correlation analysis was used to compare stochastically simulated population fluctuations to observed aspen ring widths. Spectra of simulated densities were compared among experiments and to the observed outbreak spectra. Here, the question was not so much whether January temperature was the key perturbation that modulates outbreak amplitude and phasing, but whether a density-independent perturbation such as January temperature could drive regional asynchrony in the low frequency range.

9.3 Results

9.3.1 Regional temperature patterns

All six core weather stations exhibited 14 to 20-yr periodicity in January temperature; however the five stations in central Alberta showed an additional 6 to 7-yr component (Fig. 9.1). This led to strong sub-decadal decoherence in January temperatures between northern and central Alberta (Fig. 9.2). This substantiated the initial hypothesis that January temperature, through amplitude modulation or period-forcing, might be driving sub-decadal outbreak cycles in the parkland region and super-decadal cycles in the boreal region.

The pattern of January temperature showed little coherence with spring precipitation, except near periodicities of 10 and 7-yr (Fig. 9.3). This substantiated the hypothesis that the correlation between aspen ring widths and decadal drought in the parkland (*e.g.* Fig. 3.4) might be a spurious result of winter-temperature-mediated outbreaks rather than moisture-limited aspen growth.

9.3.2 Modeling outbreak dynamics

Simulation results for the three boreal-parkland experimental trials are shown in Fig. 9.4. The stochastic dynamics (Fig. 9.4, centre column) differed substantially from the deterministic dynamics (Fig. 9.4, left column) in that deterministically damping oscillations gave way to sustained oscillations under perturbation - a result that has been noted many times (Bulmer 1976, Royama 1984, Kaitala *et. al.* 1996). For both the 10.0

and 6.5-yr endogenous parametrizations, boreal fluctuations were dominated by the exogenously driven 20-yr cycle in January temperature, whereas parkland fluctuations were dominated by the endogenous rhythm. For the 4.5-yr endogenous parametrization, dynamics in both regions were dominated by the endogenous rhythm. Periodograms of the simulated data (Fig. 9.4, right column) showed that the influence of the exogenous signal diminished with increasing frequency of the endogenous rhythm.

When boreal and parkland simulated densities were compared to aspen chronologies at Peerless L. and Cooking L., the best endogenous parametrization was the one that led to a 10-yr cycle. The simulated densities were negatively correlated with aspen ring width chronologies ® = −0.18, boreal; $r = -0.46$, parkland); however, the correlations were low due to a lack of coherence in the higher frequency ranges. In fact, in all three experiments, coherence was low in at least two of the four principal frequency bands at 20, 10, 6.5 and 4.5 years^{-1}.

Boreal simulations showed a non-stationary cycle of increasing amplitude over the period 1906-1938 which thereafter changed to a low-frequency cycle with a periodicity of about 20 years - peak density years being 1943, 1959, and 1978. Minor peaks had begun to emerge at 1950, 1966 and 1982; however, particularly strong perturbations in those years stopped them from developing into major peaks. In contrast, parkland simulations were stationary. The mean egg survival in boreal simulations was 0.81. In the southern parkland, the relative mildness of January temperatures led to a higher rate of egg survival (0.95) such that the perturbation regime did not dominate the dynamics.

Fluctuations in January temperature cohered sufficiently between the two locations that, despite the differences in perturbation severity, cycles in simulated density were phase-locked in all three experiments ® = 0.70, 0.64, 0.75 for pairs of curves in Fig. 9.4b, e, h). Notably it is the phasing of the simulated outbreaks that caused it to match aspen growth cycles; variation in amplitude did not match well.

What was it about the perturbation regimes that caused a stronger low-frequency cycle in boreal simulations? To what extent was this a result of: (1) low-frequency variability in January temperature acting as a gentle period-forcing mechanism (*e.g.* Ives *et. al.* 2000), or (2) infrequent, severe perturbations causing correlated population collapse (*e.g.* Berryman 1981)? A small simulation experiment helped address this question.

The cold tolerance threshold of populations in the parkland region was raised from −30°C to −24°C in order to lower mean egg survival to 0.81, as in boreal simulations. If the resulting dynamic reflected the 6.5-yr cycle in parkland January temperature, this would suggest that period-induction by low-frequency perturbation was more important; if, as in the boreal pattern, it displayed episodic collapse in 1950, 1966, and 1978, this would suggest that correlated collapse by infrequent and severe perturbation effects was more important.

Lowering the cold-tolerance of parkland populations resulted in a new parkland dynamic that closely resembled the pattern of episodic collapse shown in boreal simulations (Fig. 9.5). The correlation between boreal and new parkland trajectories was $r = 0.80$, indicating good agreement. Thus any period-induction effect caused by the secondary 6.5-yr cycle in parkland January temperatures was weak compared to the effect of sudden and severe perturbation.

9.4 Discussion

9.4.1 Model dynamics

9.4.1.1 Egg survival

Simulated egg survival from the three boreal perturbations was better than 0.5, which seems realistic. Indeed, the average rate of egg survival in simulated boreal and parkland populations was only slightly different at 0.81 and 0.95 respectively; yet the simulated dynamics differed tremendously between regions. This suggests that standard approaches to perturbation analysis are unlikely to detect the true effect of perturbations such as January temperature. First, empirical tests that assume independence, verticality, normality, and stationarity of perturbation effects are unrealistic. Second, critical forcing perturbations do not necessarily occur at peak density, causing a population collapse. Third, continual observation is required to detect such rare events. Fourth, perturbation effects may be difficult to measure accurately enough to deduce their importance, especially in surveys of low-density populations. Fifth, careful attention must be paid to the temporal framing of the perturbation index.

9.4.1.2 Outbreak cyclicity

Supposing January temperature does limit egg survival, the simulations suggest it may be only a few key perturbations in 1950, 1966 and 1982 that force the supposed 20-yr cycle in boreal outbreaks. This suggests that it could be severe forcing by gamma-distributed egg mortality that synchronizes boreal populations and distinguishes them from parkland populations.

This interpretation further suggests that the low-frequency boreal cycle was not a cycle at all, but merely a chance result of particularly strong perturbation effects realized on four occasions in 1911, 1950, 1966 and 1982. Given such a short population time-series, this aperiodic pattern of collapse is revealed as a broad 10 to 20-yr cycle in a periodogram.

9.4.1.3 Outbreak phasing

Was it mere chance that the three most severe boreal perturbations (1950, 1966, 1982) arrived on the heels of an outbreak? To some extent, it was not. The phasing of cycles is mostly dictated by the precise sequence of mild perturbations and has little to do with initial conditions. Thus it was the interaction between the endogenous dynamics and the autocorrelation structure in the sequence of perturbations that conspired to generate a latent 10-yr cycle with the particular phasing that would predispose it to perturbative collapse. Had the latent 10-yr cycle been phased differently, due to a different perturbation sequence, the severe perturbations might not have had the same effect in forcing an apparent 20-yr cycle.

9.4.1.4 Scale-dependent synchrony

The simulations show how, regardless of the biology of the perturbing mechanism, the same factor may have different dynamic effects in different regions. For example, given a spatial gradient in some climatic parameter, a temporal regime of perturbation may force population cycles in the severe-climate region to a certain periodicity, yet merely provide the phase-locking cue for population cycles in the mild-climate region. In such a case, phase-locking by random climatic perturbation (*i.e.* Moran's (1953) entrainment effect) acts as a global synchronizing force, but forcing by severe climatic perturbation (*i.e.* Berryman's (1981) catastrophe effect) acts as a synchronizing force locally and a de-synchronizing force regionally. In most discussions on the origin of population synchrony, these mechanisms are considered to be alternative hypotheses; however the simulations show here that they can work with or against one another depending on the scale of observation.

In the adjusted-parkland simulation experiment, no attempt was made to formally separate the independent effects of the statistical distribution of perturbations (*e.g.* gamma-distributed *vs.* normally distributed) and the spectrum of variability in the frequency domain (*e.g.* low-frequency *vs.* high-frequency). This is an important question that could be addressed through simple experimentation with a simulation model.

9.4.1.5 Predictive accuracy

The simulated outbreaks did not match reconstructed outbreaks particularly well. This might be caused by the difference between daily and monthly mean temperatures, for it is acute temperature over the coldest 2 to 4-d period in winter that determines winter egg survival, not the chronic exposure to moderately low temperatures in January (chapter eight). That they usually coincide in the long-run might explain why the monthly mean generates as good a phasing as it does. On the other hand, January temperature is probably not the only exogenous parameter that could force a period or phase-lock a cycle. Acute cold temperatures in spring, at the time of egg hatch, could produce a similar effect by the same mechanism. Chronic exposure to cool temperatures through the early larval stages could also produce a similar effect by influencing larval development rates and survival from density-independent mortality.

9.4.1.6 Structural fidelity

It should be noted that this simple model is intended only as a caricature, for, being strictly temporal, it is incapable of generating spatiotemporal phenomena, such as sub-decadal asynchrony (chapter six). As such it is unlikely to generate dynamics with multiple spectral peaks, for the only source of such complexity is dynamic interaction between the endogenous component, which can be parameterized to produce a single spectral peak, and the exogenous component, which may produce a different spectral peak. In the absence of some chance interaction, it can generate no more than two of these dominant frequencies.

9.4.2 Perturbative collapse during winter weather anomalies

In Alberta, mortality of FTC eggs is determined by a complex sequence of meteorological events that leads to a mid-winter flip-flop from Pacific to Arctic anomalies (chapter eight). Although extreme flips between Pacific and Arctic anomalies might occur only once every few winters, milder flips are a normal feature of lee atmospheric cyclogenesis induced by the Rocky Mountains (Bannon 1992, Keshishian *et. al.* 1994, Davis 1997).

Such a mechanism could be instrumental in explaining why outbreaks seem less cyclic and less well-synchronized in Alberta than in Ontario (chapter three). First, winter temperatures around the Great Lakes are less volatile due to the presence of large bodies of warm water (Changnon & Jones 1972, Scott & Huff 1996). Thus forest tent caterpillar populations there may be less vulnerable to perturbation, such that deterministic population cycles are not heavily distorted by stochastic effects. Specifically, the statistical distribution of perturbation effects in Alberta may be more gamma-distributed than normally distributed, and this should destabilize caterpillar outbreak dynamics.

Second, ENSO-scale weather cycles are stronger in western Canada than in eastern Canada and these may be associated with shifts in synoptic patterns of upper atmospheric flow affecting winter temperatures (Shabbar & Khandekar 1996, Shabbar *et. al.* 1997). Thus annual weather perturbations may be more highly temporally autocorrelated in Alberta, and theoretical investigations show that temporally autocorrelated perturbations have a strong influence on the periodicity of cyclical predator-prey dynamics (Williams & Liebhold 1995). It may not be coincidental that the most volatile shifts in winter temperature observed over the five year study period occurred during the 1996 La Niña. Interestingly, 1989 was also a La Niña winter. Meanwhile 1987 and 1992 were not only El Niño years (Shabbar & Khandekar 1996), they were years of severe forest tent caterpillar outbreak in the study area (chapter two).

Third, if winter weather patterns around the Great Lakes are less regionalized, due to the absence of topographic blocking effects, then winter temperature anomalies in Ontario may be more highly spatially autocorrelated. Theoretical investigations show that spatially autocorrelated perturbation tends to favour the synchronization of insect population cycles (Royama 1996b).

Lastly, if winter temperatures have always had a strong impact on FTC population dynamics in Alberta, it may be that major shifts in boreal outbreak dynamics around 1900 (Fig. 3.18) were a result of winter climate warming. This hypothesis would be difficult to test without knowing more about the precise nature of climate change and its impact on various FTC life stages, their natural enemies, and their primary host plants. There are obviously many other factors other than climate that might have changed over that time, including any or all elements in the food web with which FTC is intimately associated.

9.5 Conclusion

A simple, stochastic predator-prey model showed that lower January temperatures in northern Alberta may be responsible for catastrophic perturbations that force an exogenous super-decadal oscillation on top of a faster, endogenous predator-prey oscillation. Though simulated outbreaks did not match the regional pattern of reconstructed outbreaks perfectly, the phasing was approximately correct. Also, simulated outbreaks were only somewhat synchronous between in northern and southern Alberta.

Winter temperatures seem to force boreal populations into super-decadal fluctuations that resemble cycles, and they may be responsible for the phasing of parkland outbreak dynamics. However, other perturbations are probably important because simulated outbreaks were not perfectly in-phase with actual reconstructed outbreaks. On the other hand, this model is merely a caricature of the effect of winter temperature. The effects of winter temperature may be highly non-linear, partially density-dependent, and may occur over time-scales much shorter than the monthly data used here can simulate.

Future work should examine whether winter weather is responsible for both synchrony of tent caterpillar outbreaks in Ontario and asynchrony of outbreaks in Alberta. It is expected that, in parkland Alberta, winter temperature anomalies, through non-linear, partially density-dependent perturbation effects, actually helps force the sub-decadal periodicity of outbreaks. A synthetic model should be developed that tries to simulate outbreaks as a function of stochastic perturbation effects induced by fluctuations in daily winter temperature.

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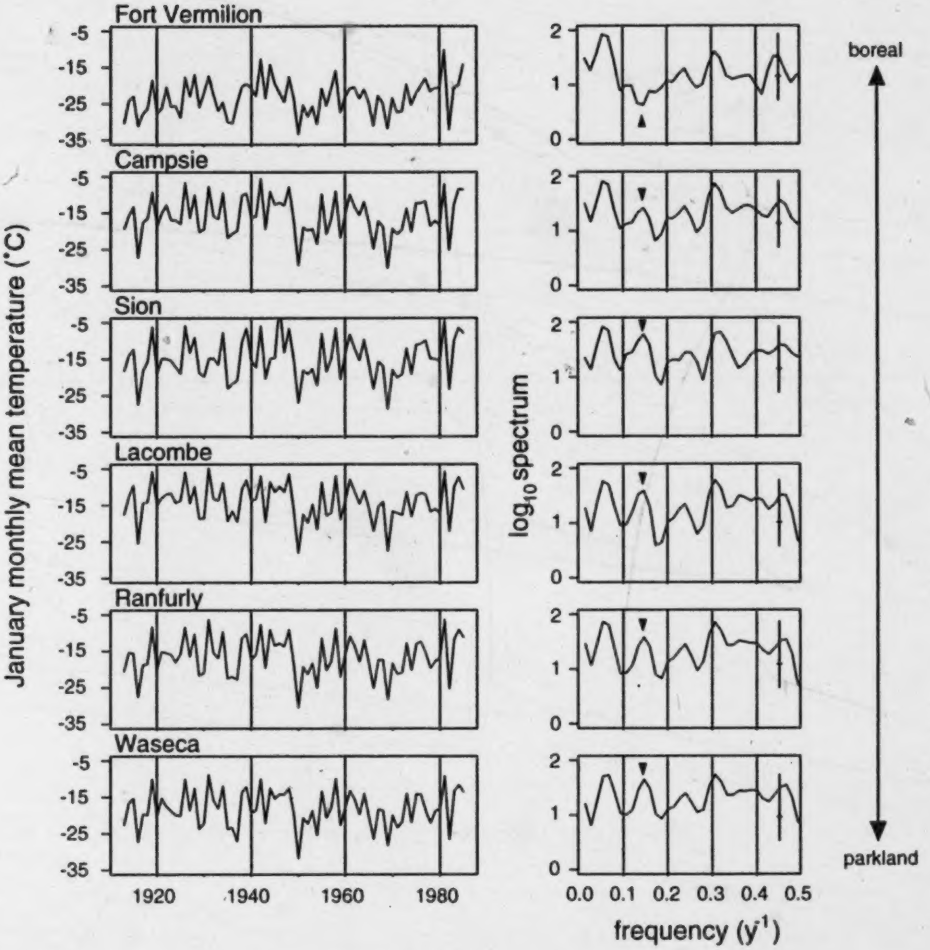

Figure 9.1. January monthly mean temperature 1913-1985 at six core weather stations. Corresponding spectra in (g) through (l) smoothed by Daniell smoother with spans = {3, 3}. Arrows indicate contrasting patterns of periodicity in the 0.1 to 0.16 y^{-1} frequency range (10 to 6.5 y) between boreal and parkland. Horizontal and vertical lines on periodograms indicate bandwidth and 95% confidence interval, assuming white null spectrum.

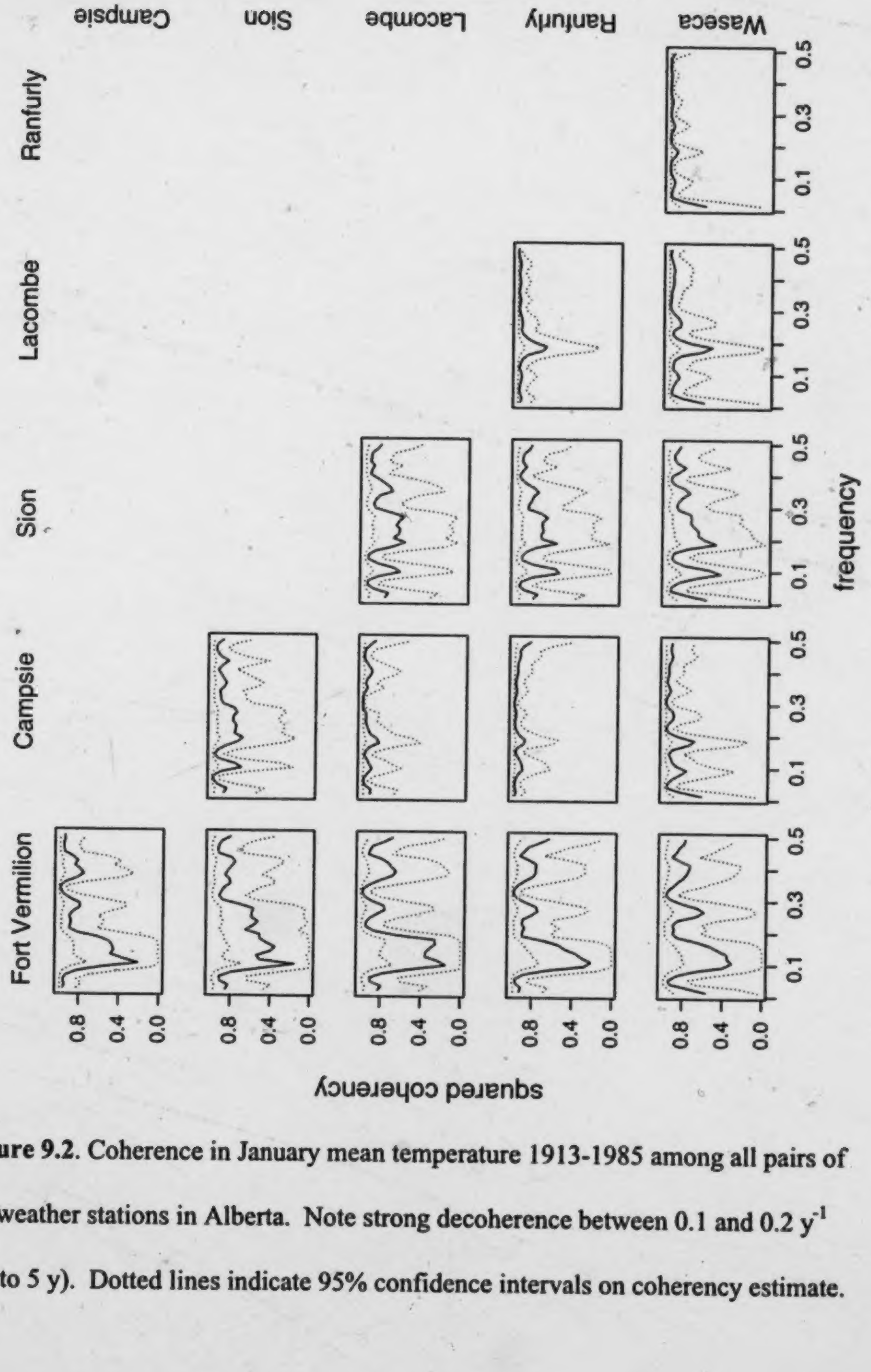

Figure 9.2. Coherence in January mean temperature 1913-1985 among all pairs of six weather stations in Alberta. Note strong decoherence between 0.1 and 0.2 y^{-1} (10 to 5 y). Dotted lines indicate 95% confidence intervals on coherency estimate.

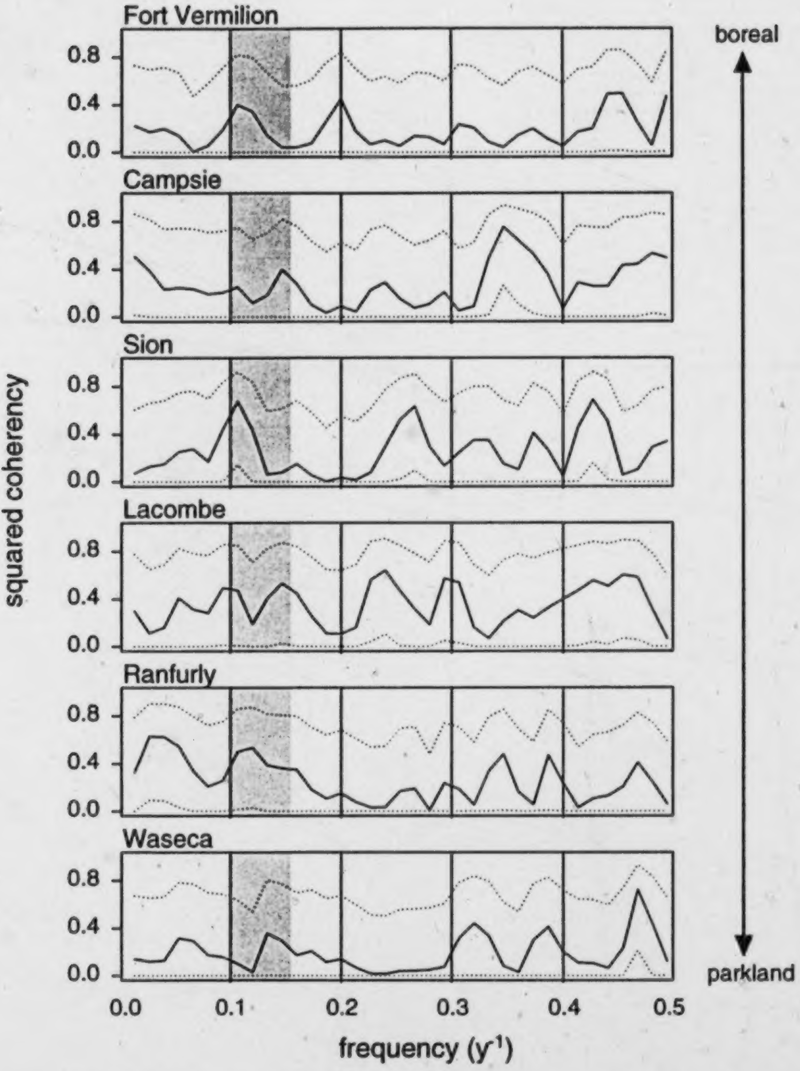

Figure 9.3. Cross-spectral coherency between January monthly mean temperature and instrumental March-June precipitation 1913-1985 for six core weather stations. Shaded bars indicate 6.5 to 10 y range in periodicity. Spectra smoothed by Daniell smoother with spans = {3, 3}. Dotted lines indicate 95% confidence intervals.

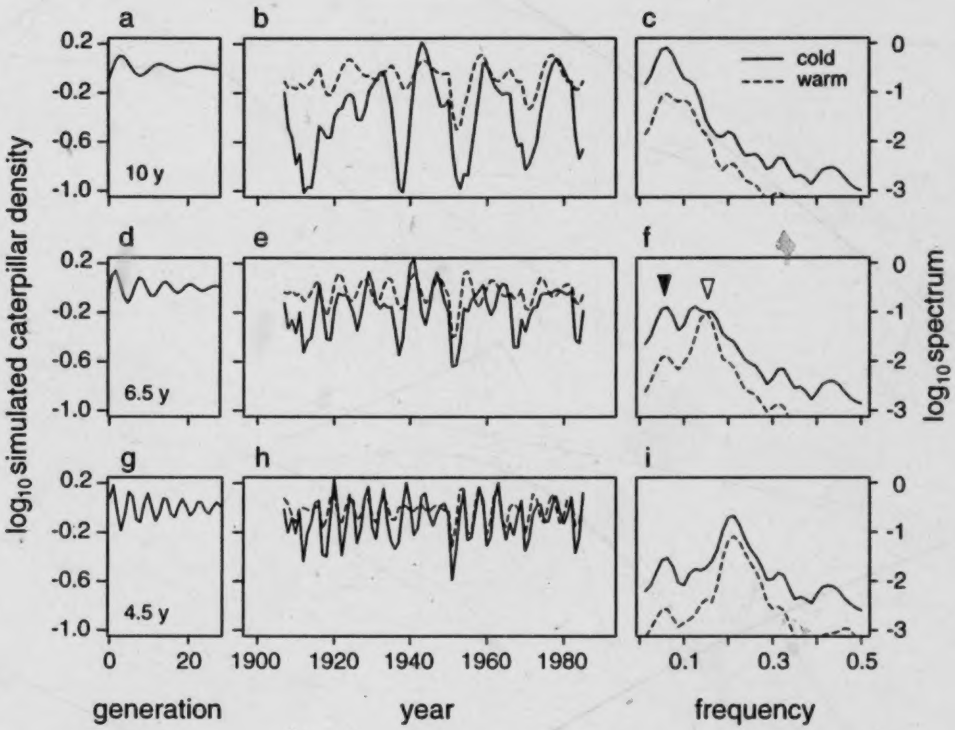

Figure 9.4. Results for three scenarios (top, middle, bottom rows) simulated with outbreak model. Left column shows determinsitic dynamics of each scenario, with damping cycles of periodicities of (a) 10, (d) 6.5 and (g) 4.5 years. Centre column shows corresponding stochastic dynamics (b, e, h) when subjected to January temperature as a perturbation regime. Right column (c, f, i) shows spectra of simulated density from stochastic scenarios. Solid curve is for northern boreal region (cold winter climate); dashed curve is for southern parkland region (warm winter climate). Spectra smoothed by Daniell smoother with spans = {3, 3}.

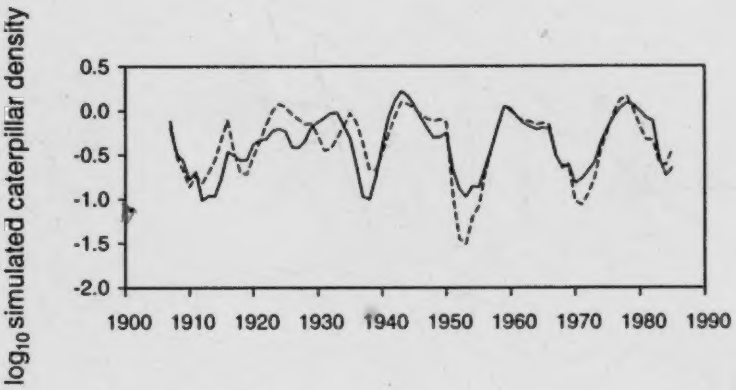

Figure 9.5. Simulated caterpillar density for the scenario where winter egg mortality is equalized between northern boreal (solid line) and southern parkland populations (broken line) by lowering the cold tolerance threshold of parkland populations from -30°C to -24°C.

10. THE EFFECT OF LANDSCAPE HETEROGENEITY ON SPATIOTEMPORAL PATTERNING IN THEORETICAL HOST-PARASITOID MODELS

10.1 Introduction

10.1.1 Effects of landscape structure on host-parasitoid interaction

The dynamics of forest tent caterpillar outbreaks seem to be under the weak, but pervasive influence of landscape structure (chapter six, Cooke & Roland 2000). There is substantial evidence that parasitoids are influenced by forest structure (Roland & Taylor 1997, Rothman & Roland 1998), but it is not clear what the dynamic implications are of alterations in parasitoid host-searching efficiency. Indeed, it is entirely possible that forest tent caterpillars themselves may be affected by forest fragmentation, and the implications here are not obvious either.

A change in parasitoid dispersal behaviour should alter the local dynamics of a host-parasitoid interaction, by changing the host equilibrium density, the oscillation frequency, etc. This can be simulated with a very simple temporal host-parasitoid model. Here, the effect of spatial variation in searching efficiency can be examined by coupling the equations in a small lattice. But in a large, dense network of interacting populations, there may be extra-local effects as well. For example, a change in host or parasitoid dispersal rates implies a change in the likelihood of spatiotemporal chaos (Kaneko 1998). In particular, a relatively high rate of parasitoid dispersal favours the evolution of chaotic population oscillations, all other things being equal (Wilson *et. al.* 1998).

More generally, even if parasitoids and hosts are equally affected by fragmentation, a reduction in dispersal rates could have global effects. A reduction in dispersal can be viewed as an increase in the spatial extent of the interaction, and an increase in spatial extent of a network implies a greater possible influence of spatial degrees of freedom on the system's dynamics. In particular, an increase in the spatial degrees of freedom may lead to spatiotemporal chaos (Kaneko 1998) or the induction of transient behaviour (Hastings 1998). If increased duration of forest tent caterpillar outbreaks due to forest fragmentation occurs *via* sub-decadal de-synchronization, is this analogous to transience-induction?

10.1.2 Simulation approach

If the spatiotemporal dynamics of a system are altered by changes in landscape structure, this argues strongly in favour of a spatially explicit approach to metapopulation modeling. At the same time, one wants to be sure that observed global dynamics are not an artifact of local peculiarities. For example, a highly resolved spatially explicit host-parasitoid interaction may be too unstable to be useful. Therefore it is important to strike a balance between realistic local behaviour and spatially explicit detail.

The aim of this chapter is to examine the effects of spatial variation in parasitoid searching efficiency on the dynamics of a coupled host-parasitoid interaction. This is accomplished using two types of models. In the first type, a two-patch host-parasitoid model is used to illustrate the effect of spatial variation in searching efficiency on host-population synchrony as a function of the predator and prey dispersal rates. Similar small-network models have been studied previously (Barbour 1990, Berryman *et. al.* 1990), but in these studies the endogenous dynamics do not vary spatially and the equations governing reproduction are linear. In the second type, the host-parasitoid interaction is extended over a dense matrix of many cells. Again, similar theoretical studies have been conducted (Ranta *et. al.* 1998, Kendall *et. al.* 2000), but the endogenous parameters did not vary spatially.

The specific questions addressed with these models are: (1) How does reducing a parasitoid's foraging efficiency affect the dynamics of a host-parasitoid system? (2) Do stable single-species models predict the same sort of complex patterning observed in less-stable host-parasitoid models? (3) Are environmental gradients likely to over-ride the process of internal self-organization and thereby influence the course of pattern selection as a system evolves from random initial states to large-scale patterning? (4) Is the frequency-locking effect of dynamic homogenization *via* dispersal sufficiently strong to synchronize completely a network of oscillators of variable periodicity? (5) Is factor analysis capable of extracting idealized patterns of asynchrony in some meaningful way?

10.1.3 Objectives of this study

The ultimate objective is to simulate observed outbreak patterns on the Cooking L. municipal grid (chapter six). Here the question is: are the observed outbreak dynamics likely to result from fragmentation effects alone? The question is "loaded" because the stochastic effects of winter temperature are not included in this modeling exercise. Nonetheless, this study illustrates the sort of patterns one might expect as a result of fragmentation.

A secondary objective is to demonstrate that spatiotemporal factor analysis used in chapter six is indeed capable of extracting the salient features of a quasi-synchronous pattern sequence. Results here may be relevant to a broad spectrum of taxa exhibiting a wide range of dynamics.

10.2 Methods

10.2.1 Model specification

Temporal models were implemented in Microsoft Excel spreadsheets. Spatiotemporal models were implemented using the R statistical package (Ihaka & Gentleman 1996, Hornik 2001). Output was animated for visual inspection (appendix two).

10.2.1.1 Two-patch host-parasitoid interaction

A two-species model of a second-order, non-linear feedback process (*e.g.* Royama 1996, Eq. 5.17a,b) was implemented in discrete time-space to simulate a 2x2 matrix of explicitly coupled host-parasitoid populations:

$$r_{it}=r_m[1-e^{-\frac{b}{b'}y_{it}}]e^{-x_{it}} \tag*{[Eq. 1a]}$$

$$r'_{it}=r'_m e^{-(y_{it}+\frac{c'}{c}x_{it})} \tag*{[Eq. 1b]}$$

$$x_{it+1}=x_{it}+r_{it} \tag*{[Eq. 2a]}$$

$$y_{it+1}=y_{it}+r'_{it}+\Sigma dy_{jt}-ndy_{it} \tag*{[Eq. 2b]}$$

where r_m and r'_m are maximum parasitoid and host reproductive rates, r_{it} and r'_{it} are parasitoid and host reproduction in generation *t* and patch *i*, x_{it}, and y_{it} are parasitoid and host densities, and *b*/*b'* and *c'*/*c* are parameters governing parasitoid host-searching efficiency and host competition. Parasitoids did not disperse between cells, while a fraction, *d*, of each host population was allowed to disperse each generation from cell *i* to cell *j* according to a King's move. With four cells, there were *n* = 3 sources of immigrants and *n* = 3 destinations for emigrants for each cell. The total population-level dispersal rate was therefore 3*d*.

Two of the four cells were parameterized to simulate efficient host-searching by parasitoids in a continuous forest (high *b*/*b'*) and two of the patches were parameterized to simulate inefficient host-searching in a fragmented forest (low *b*/*b'*). Thus the model was essentially a two-patch model in a four-population implementation. No stochastic effects were included in this model because experimentation showed the results were robust in the range of parameter space of interest.

10.2.1.2 Coupled map lattice

A single-species model of a second-order, non-linear feedback process (*e.g.*

Royama 1996, Eq. 2.20a) was implemented in discrete time-space on a coupled map lattice (*e.g.* Kaneko 1998) to simulate a gridded network of explicitly coupled oscillators:

$$R_{it}=R_m-e^{-a_0-a_1X_{it}-a_2X_{it-1}}+u_t \qquad \text{[Eq. 3a]}$$

$$x_{it+1}=x_{it}\cdot r_{it}+\frac{d}{4}\Sigma x_{jt}-dx_{it} \qquad \text{[Eq. 3b]}$$

where R_m is the $\log_{10}$ maximum host reproductive rate, R_{it} is the $\log_{10}$ net recruitment rate in generation *t* and patch *i*, X_{it} is the $\log_{10}$ host density, u_t is a random perturbation effect, and a_0, a_1 and a_2 are parameters governing local dynamics.

The dispersal parameter, *d*, represented the fraction of hosts dispersing from a population into all neighbouring cells, and was therefore not exactly the same as implemented in the two-patch model. The dispersal modeling approach here was a hybrid of several others (*e.g.* Ranta *et. al.* 1998, Wilson *et. al.* 1998) in that dispersal was assumed to be diffusive, deterministic, density-independent, and localized to the four nearest neighbouring grid cells according to a one-cell rook's move.

The deterministic component could also be described as a hybrid approach to modeling parasitism in that a highly stable single-species representation was used (*e.g.* Barbour 1990, Royama 1996) instead of an unstable, Nicholson-Bailey, two-species representation (*e.g.* Hassell *et. al.* 1992, Wilson *et. al.* 1998, Solé & Bascompte 1998). The local oscillatory dynamics here are intended to represent a spatially implicit host-parasitoid interaction (Wilson *et. al.* 1998), such that the global metapopulation dynamics are then a non-linearly scaled result (Chesson 1998) of explicit inter-population migration among highly stable sub-populations.

The model is most comparable to that of Kaneko (1998, his Eq. 4), although his studies were conducted with parameter sets (a_0, a_1, a_2) likely to generate low-dimensional chaos ($a_1 >> 1.5$, $a_2 << -1.0$), and these were not. It is unlike the reaction-diffusion class of models (*e.g.* Kareiva 1990, Solé & Bascompte 1998) in that reproduction was a monotonic decreasing function of density; no positive density-dependent reproduction was included over any density range. Hence the model contains no explicit globally eruptive mechanism and there is no chance for local diffusive instabilities.

The gridded network, at 30x30, was large (*e.g.* comparable to Hassell *et. al.* 1992, Wilson *et. al.* 1998, Solé & Bascompte 1998) relative to other studies (*e.g.* Barbour 1990, Royama 1996) because the model was intended to simulate the qualitative dynamics of forest tent caterpillar outbreaks on the high-resolution Cooking L. municipal grid. Applying the model in this context, these structural and scaling decisions reflect the tacit assumptions that: (1) the largest area over which forest tent caterpillar populations are likely to go locally extinct is less than a square kilometre; (2) populations over scales larger than this likely follow logistic growth; (3) annual dispersal is sufficiently localized that populations are not well-mixed over a 400 km^2 area; (4) environmental variability at the scale of one square kilometre could have an important influence on local dynamics; (5) environmental variability at the scale of 400 km^2 could have an important scaling influence on global dynamics.

10.2.2 Simulation experiments

10.2.2.1 Two-patch model

10.2.2.1.1 Effect of parasitoid efficiency on outbreak dynamics

Parasitoid host-searching efficiency parameter *b*/*b*' was set at 8.0 in one pair of cells and 2.0 in the second pair, reflecting a landscape-based reduction of 1/4 in parasitoid host-searching efficiency. The fraction dispersing among cell-pairs, *d*, was set to was set to 0.001. Experimentation with stochastic implementations showed this value was too small to synchronize populations through a Barbour (1990) effect. Parameters r_m, r'_m and *c*'/*c* were fixed at 1.86, 6.05, and 6.00, as Royama (1996, p. 194) did in simulating the 10 year cycle of the lynx-hare predator-prey cycle. Consequently results here are directly comparable to his non-spatial analysis.

The model was sufficiently stable that results were highly insensitive to initial conditions. Because it was completely deterministic and parameters were chosen to be far from the region of chaos, replication was not required for robustness.

10.2.2.1.2 Effect of dispersal on synchrony

The dispersal parameter was increased to simulate increased exchange among cells. Experimentation revealed that increasing *d* beyond 0.2 to 0.3 served to synchronize populations to the point of global homogeneity. Increases beyond this de-stabilized the global dynamics. Thus it was decided to focus on contrasting three carefully selected cases over a narrow range of dispersal: $d = \{0.001, 0.010, 0.050\}$.

10.2.2.2 Coupled map lattice

Values for $X_{t=0}$ and $X_{t=1}$ were initialized as a random variable distributed as $\mathbb{N}(0.0, 0.5)$. As only the canonical behaviour was of interest, a_0 was fixed at 0 and R_m was fixed at 1. The stochastic perturbation effect u_j was distributed as $\mathbb{N}(0.0, 0.04)$ in all simulations. The population-level dispersal rate *d* was fixed at 0.03 and parameter a_2 was fixed at -0.85, because the central question was the effect of landscape-dependent cell-to-cell variation in a_1 on spatiotemporal pattern formation.

10.2.2.2.1 Self-organized spatial patterning in a homogeneous environment

Initially a_1 was set to 1.5 to model a homogeneous landscape. Simulations were run a number of times over a variety of starting values and for various lengths of time in order to ensure that pattern formation was qualitatively robust. Patterns obtained here could be compared to results obtained by similar metapopulation models with less stable local dynamics. Maps of predicted density were animated (appendix two) to observe spatiotemporal patterning.

10.2.2.2.2 Effect of dispersal on synchrony

The rate of dispersal was varied over the values $d = \{0.001, 0.030, 0.150\}$, and animated patterns were examined for trends in synchrony.

10.2.2.2.3 Effect of landscape-dependent dynamics

Royama (1996) showed that the frequency of population oscillation in Eq. 3 varies as a function of a_1 (his Fig. 2.9) as does the equilibrium density (his Eq. 5.14). In order to mimic the sort of variation in oscillation frequency and equilibrium density one might expect from landscape-dependent variation in parasitoid host-searching efficiency, a_1 was allowed to vary among cells as a function of local forest cover. Note there is no one parameter in this simplistic model that maps clearly to parasitoid host-searching efficiency. Either a_1 or a_2, or both, could have been varied to simulate landscape-dependent parasitism.

Gridded values of forest cover were derived by modeling stand-wise estimates of forest cover observed across the Cooking L. municipal grid (Fig. 2.2) as a fourth-order polynomial function of geographic co-ordinates, and interpolating (Fig. 10.1, top). To complete the northwestern corner of the grid, forest cover was crudely estimated at three additional locations by looking at a 1:50 000 topographic map of the Cooking Lake area. Thus the gridded estimates of forest structure constituted a rather rough model which was nonetheless deemed sufficient for the goals of this chapter.

Parameter a_1 varied from 1.0 to 1.6 in the form of a large-scale gradient (Fig. 10.1, bottom). Given $a_2 = -0.85$, this implied gradient-like variation in endogenous local periodicity from 7.0 to 10.5 (Royama 1996). At issue here was whether patterns formed in the homogeneous simulations would be over-ridden by the introduction of spatial structure in endogenous local dynamics.

10.2.2.2.4 Recovery of simple structure using factor analysis

For S-mode spatiotemporal analysis of a 30x30 grid of data, more than 900 temporal observations are required. As this would have been too costly in terms of computing time and memory, the heterogenous environment was simulated using an 8x8 grid of 200 temporal observations.

The parameters used in this simulation were: $d = 0.08$, var(u) = 0.03, var(l) = 0.01, and $a_2 = -1.01$, with a_1 varying spatially from 1.1 to 1.6. The reason for lowering a_2 was to decrease the stability of local oscillations in order to increase the complexity of the global metapopulation behaviour. The spatiotemporal output was then subjected to unrotated factor analysis using Minitab (Minitab Inc., State College, PA) to determine whether this technique was capable of extracting the complex spatiotemporal structure known to exist. Eight factors were extracted.

10.3 Results

10.3.1 Two-patch model

10.3.1.1 Effect of parasitoid efficiency and dispersal

10.3.1.1.1 Local dynamics

The effect of reducing the parasitoid searching efficiency, *b*/*b*', from 8.0 to 2.0 was (after eliminating the first 20 transients) to increase the frequency of oscillations from 10.5 to 7.4, increase the average host density from 0.55 to 0.58, reduce the maximum host density from 1.61 to 0.95, and reduce the standard deviation in density from 0.51 to 0.18 (Fig. 10.2, top). Thus reducing parasitoid efficiency effectively "stabilized" the oscillation in the sense of reducing its variability. Stability in the mathematical sense of "extreme sensitivity to arbitrarily small differences in density" was no different.

With the dispersal rate, *d*, increased to 0.010, the magnitude of the effect was not quite as dramatic; but it was still obvious (Fig. 10.2, middle). With $d = 0.050$, host populations attacked by inefficiently searching parasitoids not only had a higher equilibrium density, they had a higher maximum density as well (Fig. 10.2, bottom).

10.3.1.1.2 Global synchrony

With the dispersal rate, *d*, set at 0.001, small phase-differences between populations living in the same landscape-types were able to persist, even though they fluctuated with the exact same periodicity (Fig. 10.2, top). With $d = 0.010$ populations within landscape-types were synchronized but populations between landscape-types failed to lock frequencies (Fig. 10.2, middle). With $d = 0.050$, the difference in periodicity was eliminated, and so was any phase difference: populations fluctuated in synchrony (Fig. 10.2, bottom).

10.3.2 Coupled map lattice

10.3.2.1 Self-organized spatial patterning in a homogeneous environment

As in the two-patch model, dispersal had a strong synchronizing effect on populations in different cells. Tendency toward synchrony was observed for all parameter sets examined. Perfect synchrony, however, was never achieved even after 600 generations with high dispersal. Instead, populations tended to cluster into localized pockets of synchrony (Fig. 10.3, top). Fluctuations were highly synchronous within these pockets, and highly asynchronous with respect to the surrounding matrix. Localized clustering patterns persisted for hundreds of generations, even in the presence of fine-scaled perturbation. Although the patterns of synchronized clustering can be seen in static snapshot-sequences (*e.g.* Fig. 10.3) they are more impressive when animated.

The location and number of synchronized pockets was found to be variable, depending on initial conditions. Small variations in initial states, however, did not lead to large differences in clustering topology. Therefore clustering was not a product of high-dimensional spatiotemporal chaos (Kaneko 1998), but was a product of an extremely long phase of transience induced by a very large number of spatiotemporal degrees of freedom (Hastings 1998).

Asynchronous local clustering occurred in the large-network model despite a highly predictable 10-year cycle (Fig. 10.3, bottom). In small-network models, each cell would synchronize perfectly to a 10-year cycle. Therefore the incorporation of many spatial degrees of freedom allows for the co-existence of both pervasively synchronized 10-year cycles and localized patches of asynchronous cycles.

10.3.2.2 Effect of dispersal on synchrony

The robust nature of the dependency of clustering on initial conditions was underscored by the fact that changing dispersal rates did not completely change the course of pattern formation (Fig. 10.4). Large, persistent patches of synchrony in the lower-right corner were particularly noticeable, and occurred in all simulations. Their position was therefore completely determined by initial conditions. In other simulations, very different initial conditions produced a very different distribution of synchrony clusters.

What did vary as a function of dispersal rate was the scale of dynamic clustering (Fig. 10.4). Higher dispersal rates led to more widespread synchronized clustering.

10.3.2.3 Effect of landscape-dependent dynamics

When parameter a_1 was free to vary as a function of forest cover, the self-organized clustering patterns disappeared and were replaced by ripples of traveling waves emanating from the fragmented portions of the grid and converging on the continuously forested band running from the bottom-left to the upper-right corner of the grid (Fig. 10.5). The appearance of these traveling waves was an illusion created by spatial variation in population cycling frequency: populations in the upper-left and bottom-right corners of the grid cycled with a periodicity of about 7 years, compared to 10 years for the central portion of the grid.

These asynchronous cycles failed to lock frequencies when the dispersal rate was set at 0.03. This led to poor global synchrony, irregular fluctuations in mean density, and a spectral signature that was less sharply periodic than in the homogeneous landscape (Fig. 10.5). Informal experimentation revealed that even unrealistically high dispersal rates could not induce synchrony *via* frequency-locking. The traveling waves were remarkably robust.

10.3.2.4. Recovery of simple structure using factor analysis

As expected, simulation on a smaller grid with a_2 lowered to -1.01 generated more robust local cycles, which led to poorer synchrony, and resulted in a heteroskedastic spectrum (Fig. 10.6). The interesting result is that factor analysis was remarkably successful in uncovering the high-frequency oscillations in the upper-left and lower-right corners of the grid and the low-frequency oscillation along the central column (Fig. 10.7).

10.4 Discussion

First and foremost, S-mode factor analysis was shown to be highly effective at extracting the landscape-based periodic structure that underlay complex patterns of traveling waves. Thus, if outbreak asynchrony on the Cooking L. municipal grid were a product of fragmentation-driven gradients in outbreak periodicity, spatiotemporal factor analysis (chapter six) would have revealed as much. The simulations here, coupled with results from chapter six, suggest that either forest fragmentation does not alter local host-parasitoid dynamics or forest tent caterpillar outbreak cycles are not caused by slow-damping local host-parasitoid population cycles.

It seems reasonable, indeed parsimonious, to conjecture that forest fragmentation might affect forest caterpillar dispersal as much as it does parasitoid dispersal. Under this hypothesis, forest fragmentation still may have a significant impact on outbreak dynamics, for simulations in the homogeneous environment suggest that reducing dispersal effectively stretches space and thereby increases the impact of spatial degrees of freedom on pattern formation. Thus, by de-synchronizing tent caterpillar population oscillations, forest fragmentation may lead to longer outbreaks, without altering local dynamics.

Such a mechanism would explain why local fragmentation seems to have extra-local impacts on outbreak duration in neighbouring areas (Cooke & Roland 2000), and it could explain the occurrence of sub-decadal outbreak asynchrony on the Cooking L municipal grid (chapter six, but see chapter seven). Indeed, it could explain why such patterning seems more prevalent in the aspen parkland than in the boreal forest (chapter six) and it could even explain why outbreaks are more poorly synchronized in the fragmented forests of agricultural western Canada (Hildahl & Reeks 1960) than in Ontario (Sippell 1962, Daniel & Myers 1995).

In contrast to the spatiotemporal simulations, the spatially implicit model revealed perfect synchrony for even low dispersal rates. Does this imply that one of these models must be incorrect? Not necessarily, for model validity may be scale-dependent. Spatially implicit small-network models might be useful when applied at large scales to explain spatially averaged dynamics, and they might fail miserably when applied at too small a spatial scale. It may be that no one model can duplicate all the important features of a system's dynamics.

There is a clear choice to be made in modeling forest tent caterpillar dynamics: (1) focus on the endogenous biology, or (2) focus on the exogenous environment. The prevailing view among natural historians is that the biological details matter - that one can not ignore, for example, the individual roles played by:

(1) specialist parasitism by at least four species of flies and two species of wasps;
(2) specialist viruses, fungi and microsporidia;
(3) generalist predation by at least five families of insects and several species of vertebrates.

This may be true, but as a *de facto* stance, it is unconvincing. There is no *a priori* reason to believe these agents can not be viewed as a single density-dependent mortality complex. If one is interested in simulating gross features of outbreak dynamics, this may be an ideal way of simplifying complexity down to a manageable level.

10.5 Conclusion

As forest tent caterpillar female adults probably tend not to disperse very far, outbreak dynamics are probably influenced heavily by spatial degrees of freedom. Thus the dynamics may be highly transient and non-equilibrial. This may explain the complexity observed in quasi-cyclic, quasi-stable, quasi-synchronous patterns of outbreak.

Forest fragmentation may alter local outbreak dynamics by altering either parasitoid or host behaviour. But even if both are equally affected, local reductions in rates of movement will serve to increase the number of spatial degrees of freedom and thereby globally de-synchronize populations. It is an open question as to whether this is the mechanism by which forest fragmentation increases outbreak duration (Roland 1993).

This brief foray into spatiotemporal simulation shows that the details regarding a model's spatial structure and its stochastic behaviour are a rich source of complexity in outbreak pattern formation. Detail in the endogenous components is not a necessary condition for the evolution of complex patterning.

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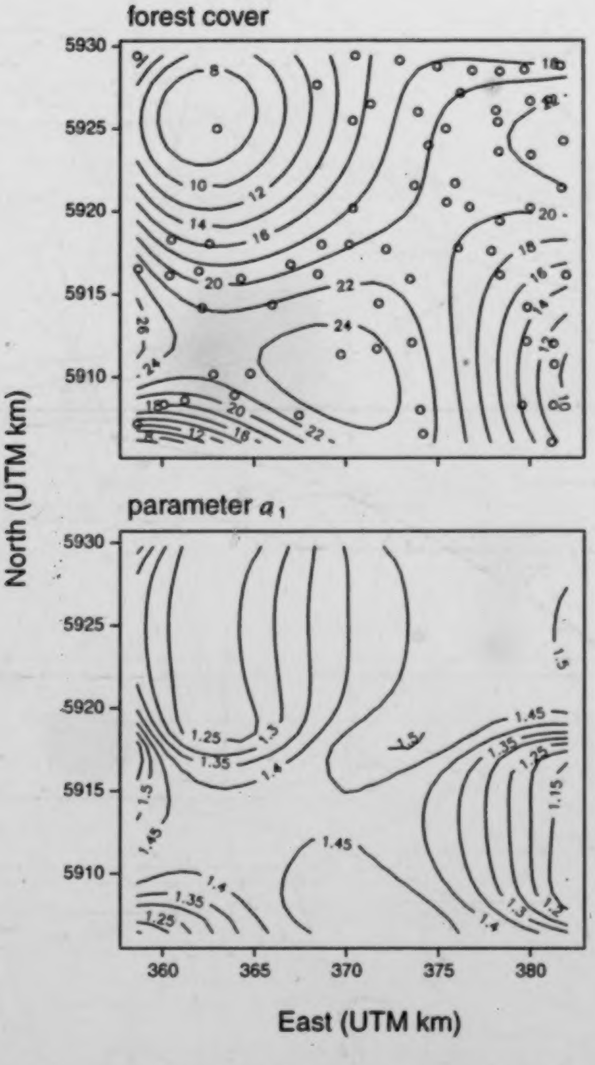
forest cover
parameter a_1
North (UTM km)
East (UTM km)
5930
5925
5920
5915
5910
360
365
370
375
380
8
10
12
14
16
18
20
22
24
26
1.15
1.2
1.25
1.3
1.35
1.4
1.45
1.5

Figure 10.1. Forest cover across the Cooking L. municipal grid (top) and landscape-dependent spatial variation in endogenous parameter a_1 (bottom). Circles indicate plot locations where forest cover was measured.

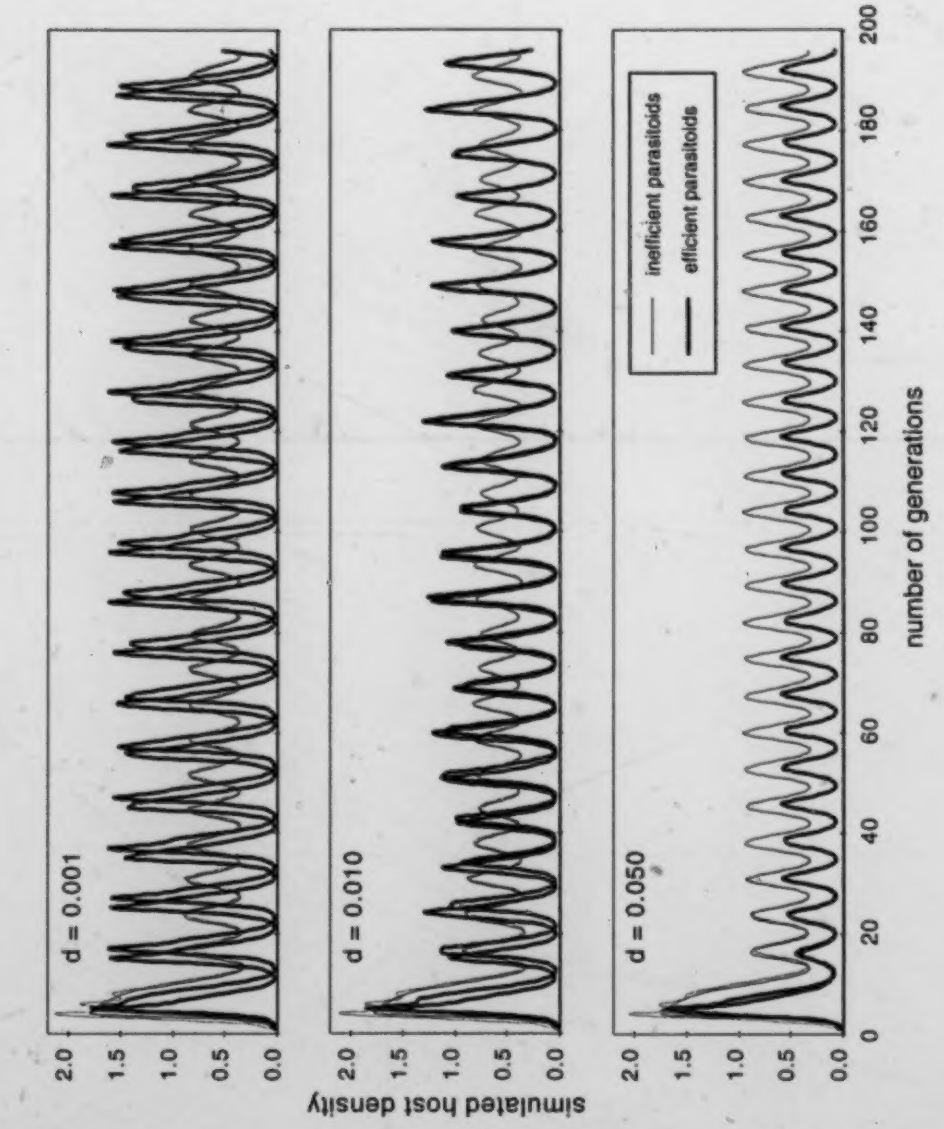

Figure 10.2. Simulation results from two-patch host-parasitoid model, showing increasing host population synchrony for increasing dispersal rate, *d*. Heavy lines indicate host populations attacked by efficient parastioids; thin lines indicate inefficient parastioids.

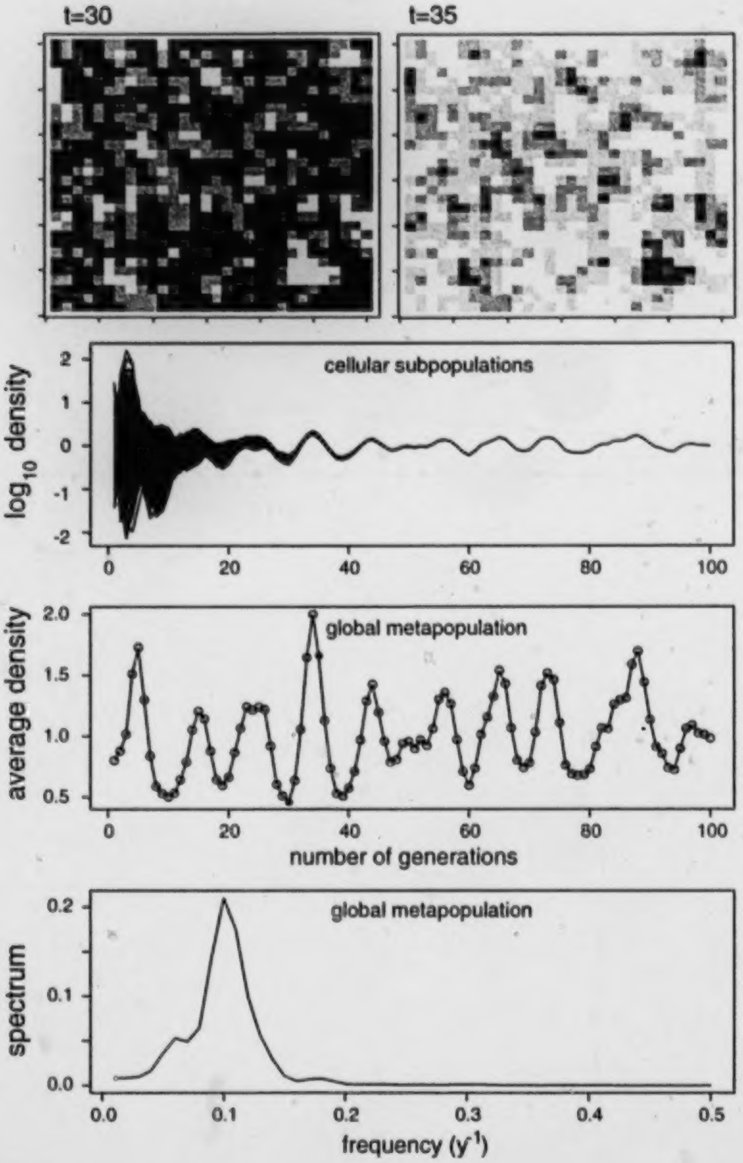

Figure 10.3. Simulated population density on a homogeneous 30x30 coupled map lattice. Spatial maps of subpopulation densities at time t=30 and t=35 (top) show persistent local clustering, despite tendency toward globally synchronous 10-yr cycle.

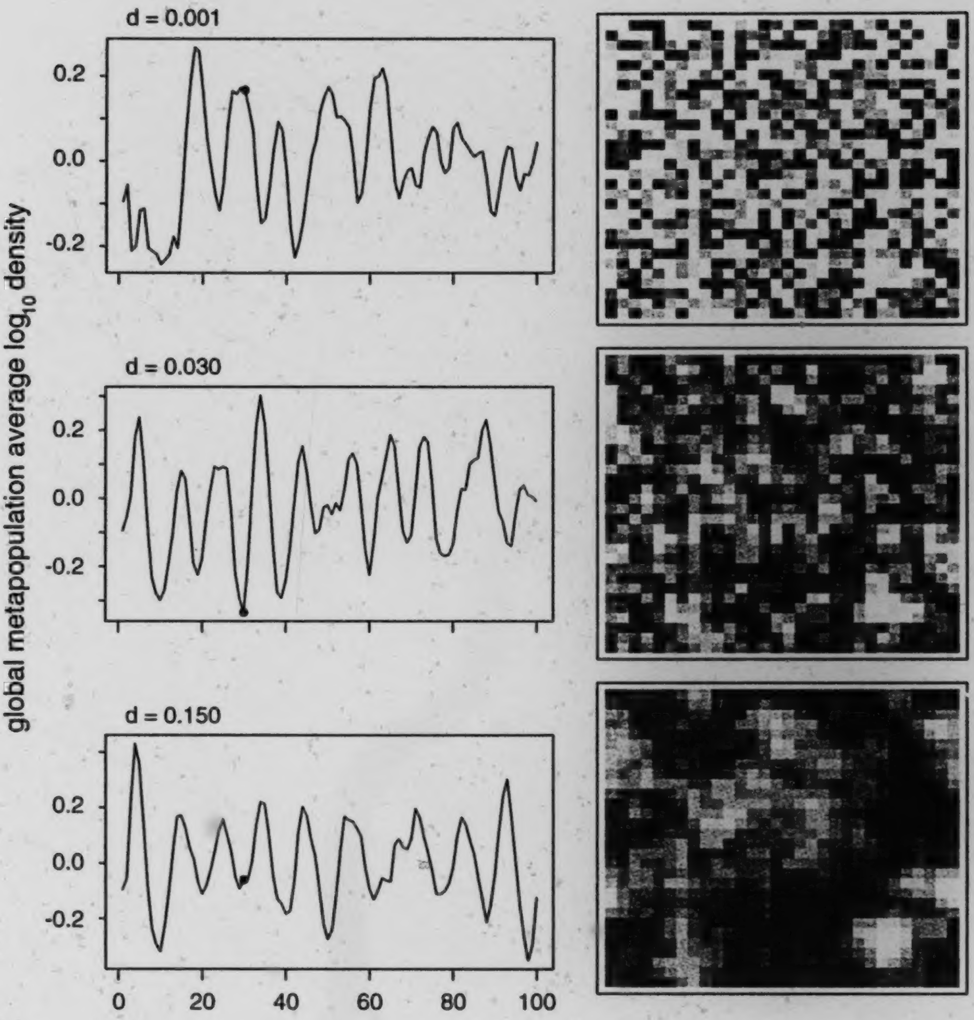

Figure 10.4. The effect of increasing dispersal rate, *d*, on the scale of dynamic clustering in a homogeneous environment. Cellular density maps are snapshots at t=30. Middle panels for *d* = 0.030 are data in Fig. 10.3. Initial conditions equivalent among simulations.

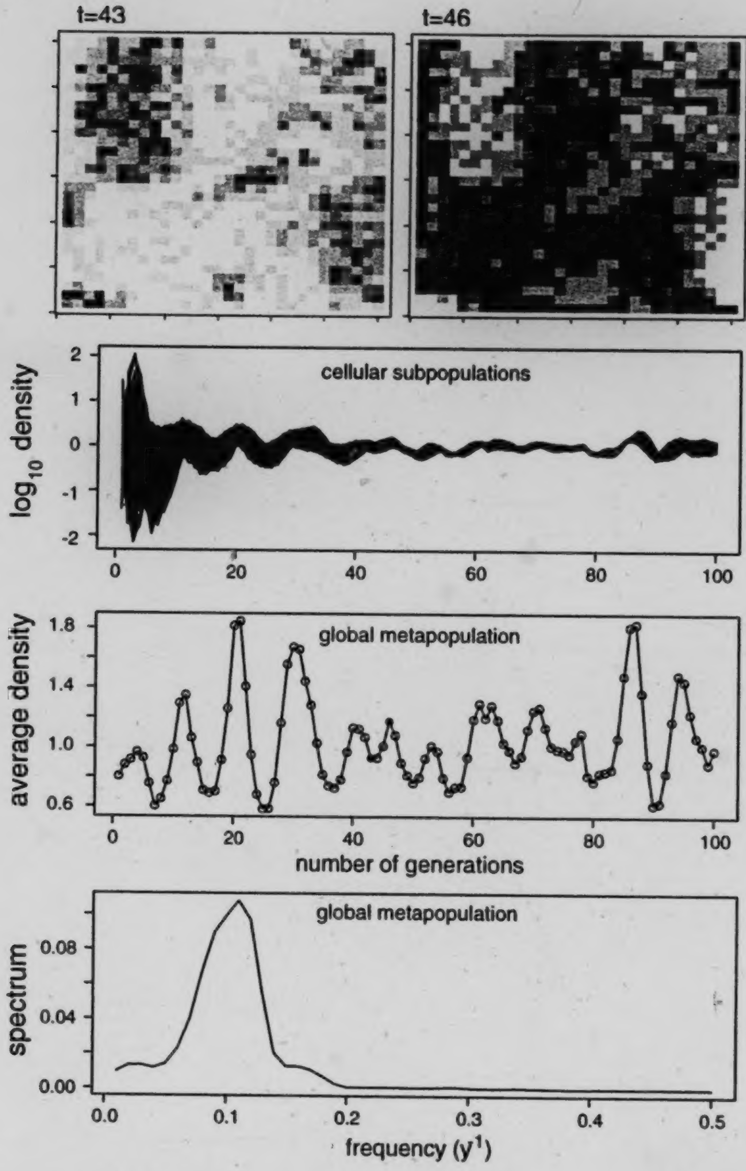

Figure 10.5. Simulated population density on a heterogeneous 30x30 coupled map lattice. Spatial maps of cellular population densities at time t=43 and t=46 (top) show persistent waves radiating from high-frequency oscillators in upper-left and lower-right corners of grid.

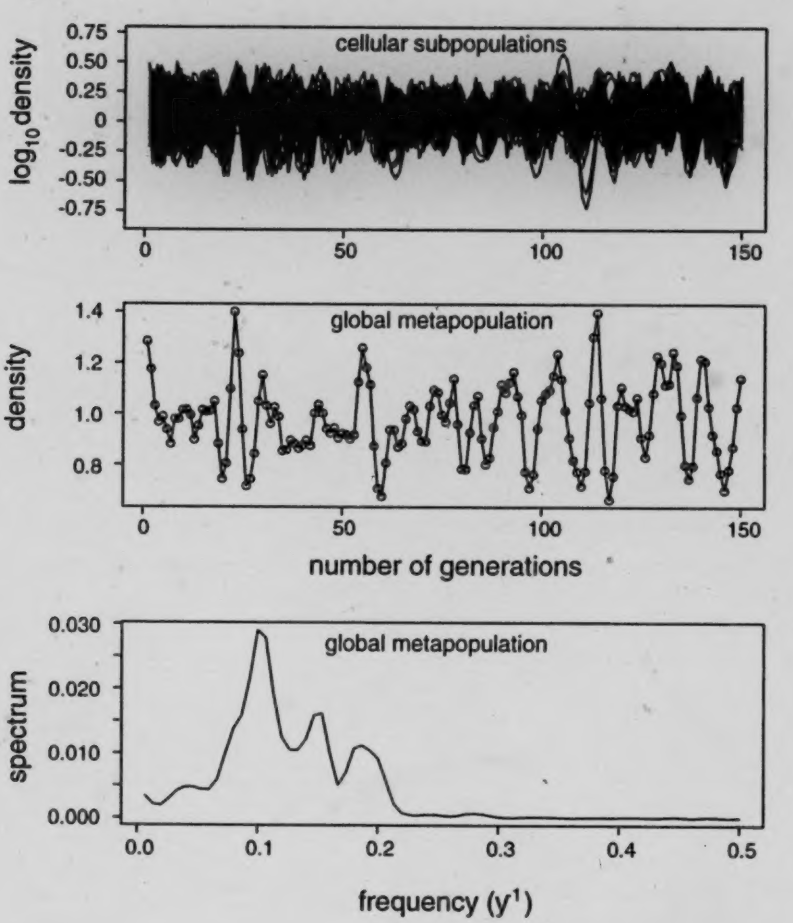

Figure 10.6. Simulated population density on a heterogeneous 8x8 coupled map lattice. Spatiotemporal analysis of data in top panel shown in Fig. 10.7.

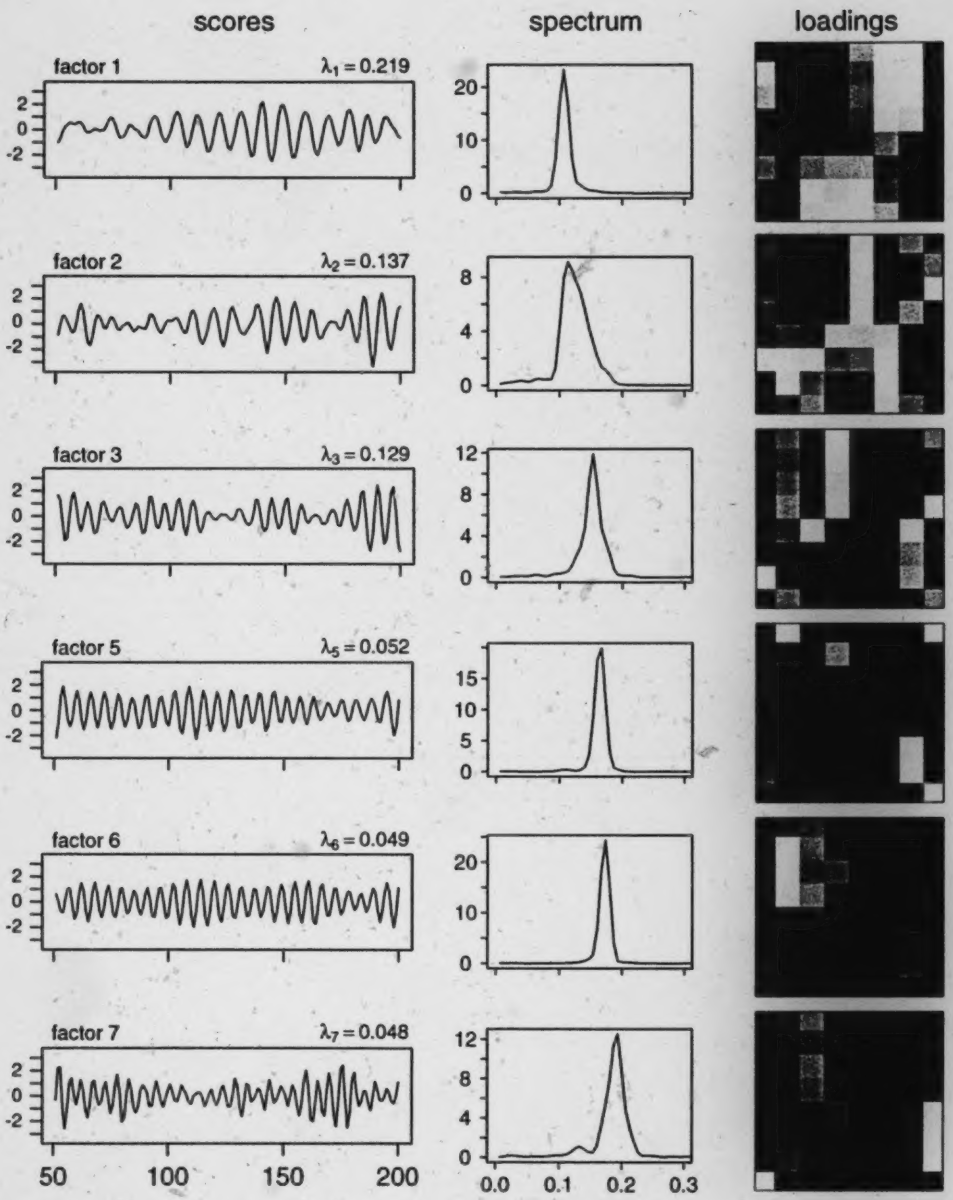

Figure 10.7. Factors 1-3 and 5-7 from unrotated S-mode spatiotemporal factor analysis of data in Fig. 10.6. Light shading indicates positive loadings.

11. CONCLUSION

11.1 Executive summary of results

Chapter 2	Aspen growth in the parkland region of Alberta is limited largely by drought and by defoliation caused by outbreaks forest tent caterpillar.
Chapter 3	Aspen growth across central Alberta is limited mainly by defoliation caused by quasi-periodic outbreaks forest tent caterpillar.
Chapter 4	Survival rates of defoliated aspen are sufficiently high that dendroecological reconstructions of past tent caterpillar outbreaks are accurate.
Chapter 5	Outbreaks of forest tent caterpillar are not chaotic.
Chapter 6	Outbreaks of forest tent caterpillar are de-synchronized by forest fragmentation and stochastic perturbation.
Chapter 7	Spatially structured detrending errors can distort patterns of outbreaks inferred from dendroecological reconstructions.
Chapter 8	Winter temperatures act as a cyclic and partially density-dependent perturbation on forest tent caterpillar egg survival in Alberta.
Chapter 9	Outbreak periodicity and phasing both may be influenced by winter temperatures.
Chapter 10	Pattern formation in spatiotemporal host-parasitoid models is strongly influenced by landscape-mediated parasitism.

11.2 Summary of principal themes

11.2.1 Outbreak reconstruction

Major episodes of reduced aspen growth in Alberta coincided closely with aspen defoliation mapped by aerial surveys from 1957 to 1998. Most of this defoliation was caused by forest tent caterpillar but some of it was caused by other species of lepidopteran defoliators.

Annual aspen growth in the boreal and mixedwood regions of Alberta is unrelated to annual precipitation during the growing season, yet aspen trees there exhibit decadal variability in ring widths (chapter three). This is not merely a weak test of the drought-limitation hypothesis, for the same test applied on parkland chronologies revealed moderate sensitivity of aspen to precipitation variability (chapter two). Not all the variation in aspen growth in boreal Alberta can be attributed to forest caterpillar. However, the bulk of the long-term, persistent, mid-frequency variability in aspen growth is undoubtedly caused by outbreaks of forest tent caterpillar.

Aspen growth in the parkland region of Alberta is influenced by decadal drought, but the effect is probably not as strong as a linear correlation suggests (chapter two), for a substantial portion of decadal variability in aspen growth has an associated joint spatiotemporal structure occurring at sub-municipal, sub-decadal spatiotemporal scales (chapter six) that can not be accounted for by a large-scale climatic factor such as decadal drought. This suggests that parkland aspen ring widths are a fair indicator of insect-caused defoliation, although perhaps not quite as good as boreal aspen ring widths. Factors such as frost and snow do have an occasional localized impact on aspen growth, but the total variability attributable to such effects, in the long-run, pales in comparison to the effects of defoliation (chapter two).

Smaller dips in aspen ring width chronologies that occurred at shorter three- to five-year intervals were initially thought to be caused by pervasive sub-epidemic population cycles that could never be detected from aerial surveys (chapter three). However later analysis revealed this was not the case. Sub-decadal dips in aspen growth appear to be caused by localized outbreaks (chapter six). The reason sub-decadal growth dips in the mean ring width chronology were lesser in magnitude than were decadal and super-decadal growth dips is that spatial averaging diminished the prominence of the localized sub-decadal eruptions. Local sub-decadal eruptions ought to be detectable from the air, but the probability of detecting such pockets is low when using a coarsely resolved network of flight lines, which is standard practice in Alberta.

The apparent amplitude of these localized eruptions may be exaggerated by stiff-spline detrending, which is a standard dendrochronological procedure that can inadvertently lead to spatial biases in detrending error (chapter seven). Patterns of sub-decadal asynchrony on the Cooking L. municipal grid (chapter six) could be a similar artifact of periodicity in such detrending errors (chapter seven). The best way to resolve this issue is through intensive sampling at each point such that detrending errors at the stem-level have an opportunity to cancel one another when averaged in a mean chronology.

It is only since the 1920's that decadal aspen growth cycles in the parkland have been well synchronized with decadal precipitation cycles (chapter two). The most plausible explanation is that moisture is becoming more limiting as a result of a summer climate warming trend.

Past disturbances are just as clear in current dendrochronological records as they were in historical dendrochronological records (chapter four), suggesting that any changes in disturbance frequency and intensity revealed in aspen ring width chronologies is unlikely to be an artifact of survivorship bias.

11.2.2 Non-stationary outbreak periodicity

Recall the earliest recorded outbreak of forest tent caterpillar in Alberta is 1902. This study showed that dendrochronology could be used to infer a province-wide outbreak occurring as far back as 1848-1850. Apparently trembling aspen in the foothills of Alberta live longer than is commonly thought. Indeed, very few trees were encountered with heart-rot. The long chronologies from Whitecourt, Peerless L. and Conklin were especially informative, for it appears there were ten more outbreaks that occurred in the seventy years prior to the confirmed 1902 outbreak in central Alberta (chapter three).

An outbreak periodicity estimate of seven years in western Canada is consistent with Leech (1944), but it is at the lower limit of 6 to 16 years suggested by Hildahl &

Reeks (1960). This difference in estimated periodicity is not trivial, for it is nearly a three-fold difference. One possible explanation for the discrepancy is differing scales of observation, for the interval between outbreaks does appear to be dependent on the spatial scale of accounting (chapter three). A simpler explanation is that the pattern of outbreaks has actually changed over time. Support for this hypothesis can be found in the spectra of aspen ring widths from Whitecourt, Peerless L. and Conklin, which indicate a clear shift in outbreak dynamics occurring around 1900 (chapter three). From 1840 to 1870 the dominant pattern was a 7-yr cycle. From 1870 to 1910 the dominant pattern was a 10-yr cycle. From 1910 to the present, the dominant pattern was complex, having both low-frequency (12.5 y) and high-frequency (3.7 y to 5 y) components (chapter three).

This change in outbreak periodicity can not be a function of forest fragmentation because the change occurred fairly suddenly around 1900, when Alberta was hardly settled. Instrumental climate data does not exist for Alberta prior to 1885 and records are very sparse until 1908, so it is impossible to test for any association here.

It is possible, however, that this is an effect of non-stationary sample-size, which is a problem inherent in any chronology developed from a set of trees varying in age. That outbreak periodicity is scale-dependent makes this possibility even more likely. For example, the early portion of a chronology is not only estimated from fewer trees, it may be based on a much smaller sampling area. This is definitely the case with the Whitecourt data. Great care must be taken in minimizing biases that result from spatially and temporally unbalanced sampling designs, and recognizing when such biases are influencing an analysis. Given that outbreak periodicity in Alberta could be said to vary from 3 to 20 years, depending on the scale of analysis, the adverse effects of an unbalanced design could be quite severe.

Independent data from Minnesota and Saskatchewan suggest that a second possible source of artificial non-stationarity, survivorship bias, seems to be low (chapter four). This is an important result because, for example, it substantiates the claim that long and severe outbreaks in Drayton Valley in 1977-1982 and 1987-1989 really were much longer and more severe and better synchronized than all previous outbreaks in that area. In other words, this pattern is unlikely to be an artifact of defoliated trees dying so much quickly than non-defoliated trees that a random sample at any given time will include far more non-defoliated than defoliated trees.

11.2.3 Effect of stochastic climatic perturbation

It is possible that the correlation between decadal precipitation cycles and decadal aspen growth in the aspen parkland (chapter two) is neither spurious nor indicative of a drought effect. It could be an indirect result of the phase-locking influence of decadal weather variability - winter temperature variability in particular - on forest tent caterpillar cyclicity. Simulations of parkland outbreaks as a stochastic function of low mean monthly winter temperatures demonstrated that this mechanism is indeed very plausible (chapter nine). However this model failed to reproduce the correct phasing and periodicity of observed outbreaks. Either the hypothesis is incorrect or the model is insufficient.

The model should be improved by using daily winter temperature data rather than monthly means. A more realistic perturbation function is also needed, for the effect of winter temperature on egg survival is unlikely to be completely density-independent (chapter eight). Increased realism in the density-dependent predator-prey representation could also improve model performance. In particular, this temporal model is incapable of generating sub-decadal asynchrony.

The spatiotemporal model (chapter ten) suggests sub-decadal asynchrony could be a natural self-organized consequence of a system dominated by the effect of many spatial degrees of freedom. The conjecture that decadal outbreaks are either phase-locked or period-forced by decadal winter temperature perturbation effects must therefore be tested with a spatiotemporal model where a host-parasitoid interaction, parameterized for clustered synchrony, is subjected to a partially density-dependent perturbation effect that is asymmetrically distributed and temporally autocorrelated.

It is readily admitted that this model is not especially simple. However it is parsimonious in the sense that it does not make a large number of unjustified assumptions. Though there are many mechanisms and assumptions, they are all supported by the data gathered in the course of this study. More importantly, it is a testable proposition.

11.2.4 Effect of forest fragmentation

Spatiotemporal factor analysis is a powerful tool capable of detecting landscape-dependent outbreak periodicity and phasing (chapter ten). However an exhaustive search for local effects of forest structure on outbreak dynamics across the Cooking L. grid revealed no clear, convincing relationship (chapter six). Outbreaks did not tend to last longer or start sooner on the fragmented portion of the grid, and they were no more frequent.

There were hints of landscape-dependent dynamics on the Cooking L. grid (chapter six), and there is reason to believe these are significant. The high-frequency asynchrony of disturbance in the area of Hastings L. was surprising and may be noteworthy in this regard, for this is the patch of discontinuously forested landscape that separates two large patches of continuous forest (the Cooking Lake-Blackfoot Provincial Wildlife, Recreation and Grazing Area and the Ministik Hills Bird Sanctuary). If the effects of forest fragmentation on outbreak dynamics are not manifest locally, but instead involve some neighbourhood around the locale, then this is the sort of weak landscape relationship one would expect. Under this interpretation it would appear that the Cooking L. grid is too small and the landscape types are too closely intermingled to observe the same sort of landscape-dependent outbreak duration reported in Ontario (Roland 1993). This interpretation would be consistent with the sort of neighbourhood effect of forest fragmentation reported by Cooke & Roland (2000) and it would explain why the effects of forest fragmentation become more clear at larger spatial scales (*e.g.* among districts as opposed to among townships, Roland 1993).

At first it was unclear whether it was forest fragmentation that was responsible for the difference in outbreak periodicity and synchrony between the aspen parkland and the boreal regions, for these could have been due to the confounding climatic gradient. Upon closer inspection, however, there appeared to be some hint of an effect in that outbreak synchrony at Drayton Valley, Whitecourt and Dixonville broke down at the transition from continuous to discontinuous forest (chapter six). Equally interesting, outbreak synchrony within discontinuously forested stand clusters in these areas was no lower than within continuously forested stand clusters. In other words, synchrony is breaking down *only* at the forest-agriculture interface, and only when each of the landscape units are large and homogeneous - again suggesting that effects of fragmentation are revealed only at larger spatial scales (chapter six).

It is therefore not only the extent and resolution of sampling that influences one's ability to measure neighbourhood effects of fragmentation of outbreak dynamics, it is also the precise, spatially explicit landscape context.

This interpretation suggests that the Cooking L. grid, given the degree of intermingling of landscape types, is too small for the detection of long-term effects of forest structure on outbreak dynamics. Furthermore, extending the grid might not help, because it is possible that the contiguous forested areas of the Cooking Lake-Blackfoot Provincial Wildlife, Recreation and Grazing Area, the Ministik Hills Bird Sanctuary and Elk Island National Park comprise a single habitat island that is too small to provide a balanced contrast with the vast matrix of agricultural landscape surrounding it. This is, however, a testable conjecture.

This interpretation also implies that Whitecourt, Drayton Valley, Frog. L. and Dixonville should be sampled in the same intensive and systematic manner that the Cooking L. area was sampled. If the measurable effect of local forest fragmentation is to de-synchronize tent caterpillar oscillations between landscape units, it should be most detectable in those areas.

In this proposed experiment, a certain amount of background synchrony-clustering might be expected from non-fragmentation effects, say due to self-organized sub-decadal asynchrony. In theory, the background effect could be estimated by sampling from continuously forested landscapes. However there is an obvious danger in assuming a continuously forested boreal grid is a suitable control for a continuous-discontinuously forested parkland grid. Two solutions are: (1) choose control and treatment grids very carefully; (2) account for uncontrolled variation by process modeling.

11.2.5 Self-organization

Spatiotemporal simulations of host-parasitoid interactions in chapter ten illustrate that the effect of spatial degrees of freedom can have a dominating influence on pattern formation: transients may take an extremely long time to decay such that rapidly-induced spatiotemporal clustering tends to persist. Under perturbation, the system may never equilibrate, instead persisting in a state of transience (Hastings 1998).

It is a highly speculative *ad hoc* proposition to suggest that sub-decadal synchrony of FTC outbreaks is a product of such a self-organized partial-clustering mechanism. But the possibility cannot be ignored, for it cuts at the very heart of the eruptivity debate. Is it this seemingly spontaneous formation of localized, asynchronous, sub-decadal outbreaks that has led to the widespread belief, especially in western Canada, that an eruptive mechanism must be driving the occurrence of forest tent caterpillar outbreaks?

The issue is crucial because it bears directly on some earlier concluding remarks. For example, the discovery of sub-decadal minor disturbances in aspen ring widths in chapter three argued against the hypothesis that outbreak cycles in Alberta are caused by the same simple predator-prey interaction that might explain super-decadal outbreaks in Ontario. There it was concluded that:

> "If the principal oscillation of forest tent caterpillar populations is due to lagged interactions with parasitoids, then the nature of the interaction must be substantially more complicated than most models assume."

To be strictly correct, the phrase "most models" should be revised to read "most *small-network* models" because patchy sub-epidemics should be expected from large-network host-parasitoid models.

Similarly, under a self-organization hypothesis the following conclusion, from chapter three, about population connectivity and synchrony would also have to be revisited:

> "The weakly asynchronous outbreak patterns at the local scale and the highly asynchronous patterns at the regional scale suggest that outbreaks are not merely the result of limit cycles driven by a simple predator-prey interaction. This sort of weak synchrony is not predicted from theoretical models of population dynamics that take into account Moran's effect of synchronization of intrinsically identical oscillators *via* spatially autocorrelated independent random perturbations and Barbour's effect of synchronization of a metapopulation *via* dispersal among sub-populations. Therefore, even at small spatial scales, it is questionable to what extent host and parasitoid populations are:
>
> (1) inter-connected by migration among forest patches;
> (2) jointly influenced by spatially autocorrelated perturbations;
> (3) intimately coupled in a specialist predator-prey interaction."

To be strictly correct, a revised statement might read: "This sort of weak synchrony is not predicted from *small-network* theoretical models ..." because synchrony-clustering ought to be expected from large-network host-parasitoid interactions.

The fundamental problem with a self-organization hypothesis of FTC outbreaks is that sub-decadal asynchrony on the Cooking L. municipal grid persisted for only short time (chapter six) whereas the model predicted persistent synchrony-clustering (chapter ten). Of course, the model also predicted that synchrony-clustering would give way to persistent patterns of traveling waves under landscape-based spatial heterogeneity in endogenous local dynamics (chapter ten), and this wasn't observed either (chapter six).

Either the self-organization hypothesis is wrong, or the fragmentation hypothesis is wrong, or the models need improvement. These hypotheses should be re-examined with a hybrid model that simulates the partially density-dependent effect of winter temperature (*e.g.* chapter nine) on the stochastic spatiotemporal dynamics of a host-parasitoid interaction (*e.g.* chapter ten). It is expected, for example, that traveling waves would break down more readily under stochastic perturbation if population oscillations were parameterized for rapid-damping.

11.2.6 Dispersal and connectivity

The spatiotemporal simulations showed that, in a homogeneous landscape, varying the dispersal rate served only to adjust the scale of synchrony-clustering (chapter ten). If the effect of forest fragmentation is to reduce population connectivity, then this should cause a reduction in the scale of synchrony-clustering. One way of viewing this result is to conclude that increased dispersal effective shrinks the size of the arena.

If dispersal rates are low, as is expected in the case of forest tent caterpillar, then detecting such effects in real populations may require sampling at a very high resolution. Consider, for example, the clarity of wave patterns observed in simulations on a 30x30 grid (Fig. 10.5) compared to those on an 8x8 grid (Fig. 10.7).

From these simulations one may conclude that there is no reason to believe that it *must* be through parasitoid movement that forest fragmentation de-synchronizes and lengthens forest tent caterpillar outbreaks. The same effect could occur even if it is only caterpillar movement that is impeded by forest fragmentation. To generalize: if one or the other is more affected by fragmentation, then local dynamics should be altered; if both are equally affected, then global synchrony should be altered.

11.2.7 Dynamic stability of population fluctuations

If the pattern of stability in detrended aspen ring widths is indicative of the pattern of stability in forest tent caterpillar populations, then outbreaks are not chaotic at the municipal scale (chapter five). There seems to be, however, a large-scale spatial gradient in the degree of global stability. Although fluctuations in aspen ring widths seemed more erratic in the boreal mixedwood chronologies, non-linear stability analysis showed that they were globally stable. It was in the aspen parkland where the dynamics exhibited the lowest global stability.

The pattern in local stability was almost the opposite: the parkland municipalities, which showed low global stability, showed no episodes of short-term chaos while the boreal municipalities, which showed high global stability, showed episodic short-term chaos. It was these episodes of short-term chaos that led to the erratic temporal patterns observed in the boreal chronologies.

It is unclear how these patterns in stability should be interpreted biologically, but the distinctness of these patterns demands further investigation. Greater global instability observed in parkland chronologies might be an artifact of: (1) more intensive sampling in the parkland municipalities, or (2) sampling both continuous and fragmented landscapes, which seem to have different dynamics. These possibilities should be investigated by: (1) using a more balanced sampling design (equal numbers of plots and sizes of areas sampled among municipalities), and (2) conducting stability analysis at multiple spatial scales. Of course, the first issue needing resolution is whether the accuracy of stability analysis using the method of Ellner & Turchin (1995) is constrained by the quality of the models used to simulate aspen chronologies. If the quality of the models varies spatially, then spatial patterns in stability estimated from the models are suspect.

The pattern of borderline stability in outbreaks on the Cooking L. grid (chapter five) should be considered in a spatial context. Individual outbreaks varied in the number and location of nucleation points, the direction of spread, and the location of initial collapse, but that no explanation was found for these patterns (chapter three). A worthwhile conjecture is that it is a result of either spatially varying stochastic perturbation or non-linear dynamics.

The action of sensitively temperature- and density-dependent egg survival (chapter eight) illustrates the sort of biological mechanism that: (1) might de-stabilize an otherwise stable host-parasitoid oscillation, and (2) could lead to estimation errors in modeling for non-linear stability analysis. Parasitism is another process that is likely to be sensitively temperature-dependent and could serve as a source of stochastic perturbation or non-linear dynamics.

The only good mechanistic argument against low-dimensional chaos is that outbreaks do not seem to decline solely as a result of a caterpillar-natural enemy interaction. Almost always there is a stochastic event that assists collapse: a cold winter reducing egg hatch; a stormy spring reducing colony establishment; a late spring frost reducing foliage availability; a long, cold spring prolonging larval development and increasing early larval predation by generalist species. If the specialist host-parasitoid/host-virus interaction is so highly non-linear that it leads to chaotic oscillations, then the regular involvement of density-independent perturbations in outbreak collapse would be hard to explain.

11.2.8 Non-linear perturbation effects

The notion that stochastic perturbations may be non-linear in impact is not a common one. Royama (1996, p.40) proposed the concept, but did not suggest a means of quantifying the effect:

> "a quantitative analysis of a process involving lateral or non-linear perturbation is not easy. Thus, provided that their effects are comparatively small, we may resort to an approximation by the simplest vertical perturbation scheme. Nonetheless the conceptual distinction between the three types of perturbation would still be useful for qualitative understanding of population dynamics, such as the mechanism causing an insect outbreak, even if a quantitative analysis is difficult."

In his quantitative analysis of classic cases, he assumed that non-linear perturbation effects are small in every case except for that of the spruce budworm.

It is beginning to appear as though non-linear perturbation effects may play a significant role in mediating forest tent caterpillar population fluctuations. Unlike the spruce budworm scenario, however, the envisioned mechanism does not principally involve stochastic-deterministic perturbations of alternate hosts on parasitoids; it involves the stochastic effects of climatic fluctuations. If this is true, it would create many difficulties for analytical modeling of life-table data.

If non-linear stochastic perturbation effects are important in assisting forest tent caterpillar outbreak collapse, then spatial variation in perturbation impacts may have enduring residual effects on subsequent pattern formation. This could explain seemingly spontaneous outbreak pattern formation on the Cooking L. grid.

More generally, if one assumes that forest fragmentation on the Cooking L. grid leads to globally weakened synchrony, then non-linear perturbation effects could explain why outbreaks do not appear to last longer in the aspen parkland: high densities are attained so much more quickly under fragmentation that populations quickly become vulnerable to perturbation. The anticipated longer-lasting outbreaks therefore never materialize because of perturbation. According to this theory, outbreaks are more *frequent* in the aspen parkland because of forest fragmentation. Under this scenario, the long-term total number of years of severe defoliation would be expected to be higher in fragmented forests - even though average outbreak duration would be shorter.

11.2.9 Eruptivity

The dynamics of FTC outbreaks are eruptive only in the broadest sense of the term. Taken in its narrow sense, eruptivity - which is the tendency for outbreaks in one locality to spread to another by means of autocatalytic population release from an endemic equilibrium state - is not a *necessary* proposition to explain poorly synchronized forest tent caterpillar outbreaks in Alberta. Outbreaks may be eruptive, but this is not necessarily so. To be perfectly clear: one cannot categorically state that "forest tent caterpillar outbreaks exhibit eruptive dynamics" as though it were a matter of fact.

The best argument for an eruptive mechanism affecting forest tent caterpillar outbreak occurrence is the discovery of fine-scaled sub-decadal asynchrony associated with shifting patterns of outbreak (chapter six). An eruptive hypothesis, however, must explain why these presumed eruptions do not spread to adjacent areas that have not experienced outbreak for quite some time.

11.2.10 Complexity

Insect outbreaks are complex phenomena. It is true that simple models can generate complex dynamics; however simple models are unlikely to generate very realistic behaviour when used to model individual systems. Simulating complex phenomena observed in a specific system requires a sophisticated model. The practical issue in a system modeling exercise is to determine which aspects should be simplified and which should be represented in great detail.

The spatiotemporal simulations in this study suggest that complexity arising from assumptions about a model's spatial structure and its stochastic behaviour are sufficient to generate complex outbreak patterns. Detail in the endogenous components is not a necessary condition for the evolution of complex patterning. Consequently, spatiotemporal stochastic simulation of a simplified predator-prey interaction appears to be a fruitful avenue for future research into the mechanism underlying forest tent caterpillar outbreak dynamics.

11.3 Future research

The broad nature of this study leads to numerous and varied possible avenues for future research. Rather than draw up a long list of tangentially related questions, it seems more valuable to focus on a few very specific questions that are most critical to the sweeping implications of this study.

11.3.1 Field surveys

First and foremost, the inherently conjectural nature of outbreak reconstruction demands continuing efforts at validation. There are simply too many factors that affect plant growth to blindly accept the proposition that forest tent caterpillar outbreak dynamics can be inferred unambiguously from aspen growth dynamics.

With the baseline aspen ring width chronologies established in this study, additional sampling can be done quickly and cheaply by extracting cores instead of sectioning discs. Typically, when using cored samples, low cross-correlations in ring widths, which are expected under meso-scale disturbance, are troublesome because it is then difficult to cross-date any samples that have tiny, intermittent, or missing rings. But now that the approximate scales of tent caterpillar outbreak synchrony are known, future dendrochronological work in aspen will be that much easier, for one can expect poor ring-width cross-correlations among samples from different outbreak synchrony clusters and one can increase the sampling resolution to accommodate asynchrony in those areas. The more highly resolved the spatial scale of sampling, the easier the task of dendrochronological interpretation becomes because correlations among width chronologies decay smoothly instead of abruptly.

The single most important recommendation that will emerge from this study is to sample aspen across the province uniformly and at high resolution. Given the surprising pattern of sub-decadal asynchrony that emerged in the current study, this is a Baconian endeavour likely to bear fruit. For if current thinking about the role of spatial degrees of freedom in transience-induction is correct, complex patterns of spiral waves and spatiotemporal chaos are rather likely to emerge.

Understandably, large-scale sampling at high-resolution may be viewed as an expensive proposition, so sampling priorities are listed according to their informational value.

11.3.1.1 Targeted validation

The municipalities sampled in the current study were chosen to form a 3x3 grid, convenient for population modeling, with no regard for proximity of weather stations or presence/absence of defoliation. This section points out specific locations where anomalously high or low precipitation and non-FTC defoliation in specific years should lead to informative patterns of aspen ring widths. Sampling at these locations is a high priority because estimating background variability due to non-FTC effects will help validate the outbreak reconstructions presented in the current study.

Some of the sampling points listed here - especially those where large aspen tortrix defoliation was severe - lie outside the current grid. The ones lying inside the current grid are obviously a higher priority.

11.3.1.1.1 Estimating background effects

11.3.1.1.1.1 Drought

Eight locations have weather stations with highly continuous and complete records: Wabasca L., Slave L., Ranfurly, Waseca (Saskatchewan), Fort Vermilion, Campsie, Sion, and Lacombe. Sampling at these precise locations would maximize the observed response of aspen to precipitation variability by eliminating estimation errors in kriging.

The following locations have weather stations with more limited records but exhibited at least one year of extremely low spring precipitation that ought to have influenced aspen growth: Radway 1950, Hughenden 1941 & 1958, High Prairie 1958, Kinuso 1938, Falher 1967. As these also happened to be years of large-scale forest tent caterpillar outbreak, it might not be clear, from these samples alone, whether small ring widths were due to low precipitation or defoliation. In contrast the following locations exhibited extremely low spring precipitation in non-outbreak years: Ranfurly 1922 & 1945, Wabasca 1922, Radway 1945, Lessard 1945, Kinuso 1985, Slave L. 1985, Tulliby L. 1985.

11.3.1.1.1.2 Large aspen tortrix defoliation

Large aspen tortrix, *Choristoneura conflictana* (Walker), frequently occurs in association with the forest tent caterpillar, such that it is impossible to partition defoliation impacts into separate components. It is not known how much variation in aspen growth is attributable to defoliation by each species, and it is not even possible to measure this using existing historical data because these defoliation maps lump both species together. It is, however, possible to estimate the maximum possible confounding effect by measuring growth reduction in those areas known to be severely defoliated by large aspen tortrix exclusively. If the maximum possible effect of species-confounding is small, then the tortrix issue is a moot point.

From 1978 to 1994 the following locations exhibited at least one year of severe defoliation by the large aspen tortrix: Wood Buffalo Park, Red Earth Creek, High River, Keg River, Peace River, Grande Prairie, Clear Hills, Birch Hills, Hinton, Rocky Mountain House, Calgary, Camrose, Millarville, Stettler, Cypress Hills, Waterton Lakes, Wainwright.

Although Bruce's spanworm, *Operophtera bruceata* (Hulst), occurs throughout Alberta, careful examination of annual Forest Insect and Disease Survey records from 1978 to 1994 revealed substantially fewer instances of localized outbreaks for this species compared to large aspen tortrix.

11.3.1.1.2 Sensitivity analysis

Aspen trees seem to be a more sensitive indicator of defoliation impacts than are aerial defoliation surveys (*e.g.* Fig. 2.14). This is a critical issue because sub-decadal outbreak asynchrony, for example, is not revealed in aerial defoliation maps. The sensitivity of aspen responses to forest tent caterpillar population density could be tested in several ways: (1) sampling in areas that have aspen forest but never seem to be defoliated, to see if these actually were lightly defoliated during outbreak years; (2) sampling known isolated pockets of defoliation in the southern aspen parkland, to see if localized defoliation in non-outbreak years is detectable; (3) sampling in urban or grassland areas where forests are extremely fragmented and outbreaks are rare.

11.3.1.1.2.1 Topographical gradient

There are three broad areas where a topographical gradient seems to lead to a gradient in outbreak severity. High elevations throughout the Swan Hills, the Pelican Hills, Edson, and the foothills of the Rocky Mountains are rarely defoliated but aspen forests there probably support endemic or locally "eruptive" populations of forest tent caterpillar. These populations are expected to cycle in synchrony with outbreak populations in neighbouring lower areas, but they may be poorly synchronized.

11.3.1.1.2.2 Known outbreak refugia

In between the massive province-wide outbreaks of 1937-42 and 1957-62 there were five instances of isolated and ephemeral pockets of defoliation at four locations in the southern aspen parkland: Thorsby 1946, Nobleford 1948 & 1950, Rimbey 1951, Mile 103, Mackenzie Highway 1953-56. These locations should exhibit strong effects of defoliation in the specified years. In contrast, aspen from the surrounding area should exhibit no effects of defoliation, especially in those years. All locations deep in the aspen parkland should exhibit strong precipitation responses

11.3.1.1.2.3 Gradients of extreme fragmentation

Being far removed from large forests, outbreaks in extremely fragmented landscapes should be weak, rare and poorly synchronized with respect to the nearest forested synchrony-cluster. Population densities would then be at the limit of detectability with dendrochronology.

First, the Cooking L. grid should be extended westward to include: Edmonton, Stony Plain, Spruce Grove, Sherwood Park, and St. Albert. Second, the provincial grid should be extended southward by sampling at Red Deer and Wainwright.

11.3.1.2 Novel application

11.3.1.2.1 Outbreak dynamics

11.3.1.2.1.1 High-resolution Cooking L. grid

The high-frequency asynchrony of disturbance in the area of Hastings L. was surprising and particularly noteworthy. This illustrates the sort of fine-scale structure that might exist on other parts of the grid at finer spatial scales. That there is always at least one plot on the grid where aspen growth is abnormally low suggests that higher-resolution sampling should reveal more such instances. If these refugia are shown to extend over the stand level it would help refute the argument that these are merely endogenous stem-level growth anomalies.

11.3.1.2.1.2 Replicated municipalities on provincial grid

That the Cooking L. grid was vulnerable to drought effects suggests that similar grids should be sampled in municipalities not vulnerable to drought, such as Whitecourt or Athabasca.

That sub-decadal outbreak synchrony occurs over areas less than 20x20 km suggests there are huge gaps on the provincial grid that ought to be sampled, especially at Valleyview and Simonette.

11.3.1.2.1.3 Synchrony breakdown

The sampling resolution should be higher wherever synchrony breaks down or is expected to break down. Interesting possibilities include sampling between forest clusters and sampling on either side of major highways. If clearings or roads act as barriers to dispersal, populations separated by such barriers should not be well synchronized.

11.3.1.2.2 Forest-level volume losses

Volume losses in canopy trees may be compensated to some degree by gains following disturbance, particularly in the understorey. Such effects should be quantified because they may influence the predictions of wood supply models upon which harvest schedules are based.

11.3.2 Experiments

11.3.2.1 Endogenous stand-level trends

It is not at all clear that the detrending techniques employed in this study provide an unbiased estimate of low-frequency variability in growth due to forest tent caterpillars. Sampling in areas where stand histories are well-documented or artificially controlled would help to understand the impact of defoliation in the absence of unknown environmental and endogenous variability. Sampling in areas without tent caterpillars would show natural patterns of growth in the absence of defoliation. Ideal natural situations may exist in upland areas that do not seem to experience outbreaks, such as Swan Hills.

11.3.2.2 Effects of defoliation and drought and interaction

A controlled experiment is required to evaluate the independent and synergistic effect of drought and defoliation. The synergistic component is particularly important because of the coincident decadal cycles of precipitation and outbreaks in the aspen parkland.

11.3.2.3 Effects of cold on egg hatch

Several propositions made in this study need to be investigated or corroborated through formal experimentation:

(1) warm weather (above 0°C) immediately prior to cold weather (less than -35°C but higher than the LT_{50}, assumed to be roughly -41°C) will lead to higher egg mortality than

cold treatment alone;

(2) excess moisture on the surface of the egg mass prior to cold treatment will cause higher mortality and could influence the pattern of mortality within an egg mass

(3) larvae that are starved or fed non-host foliage will produce adults that lack the parental resources to confer cold-tolerance on their offspring;

(4) after natural selection by a cold-weather anomaly, the surviving population might be more cold-tolerant or cold-avoidant than the original population.

Results here would help in developing an egg hatch hazard function that could be applied to daily weather data to simulate the seasonally-integrated generational risk of egg mortality. Applied over many years of temperature data, such a hazard function would provide an adequate stream of perturbations that could be employed in stochastic simulations of tent caterpillar population dynamics. This would be better than simply using lowest daily minimum temperature and much better than using mean monthly temperature in January.

11.3.3 Modeling

11.3.3.1 Environmental data

Spatial kriging is inadequate for reconstructing a spatiotemporal series of temperature of precipitation because, when applied independently to a sequence of maps, it ignores temporal structure among maps. This is obviously a problem if one wants to estimate the temporal structure of a variable at a point for which there are no samples. Here, the estimated values should have a temporal structure that is not unlike the temporal structure in surrounding data points. The greater the temporal structure, the more important it is to use a method that will faithfully reproduce it. A spatiotemporal estimation procedure needs to be developed.

11.3.3.2 Spatiotemporal outbreak simulation modeling

A synthetic conceptual model has been proposed but a quantitative implementation has not. All the essential elements have been spelled out over the course of this study, and a few of them have been incorporated in the simulation trials, but they need to be integrated into a single, synthetic, quantitative, spatiotemporal model, which can then be compared to the inferred outbreak patterns at both municipal and provincial scales

. If this model is unable to accurately reproduce gross features in observed outbreak patterns, then some components have been oversimplified. Candidate processes that might require additional theoretical and empirical investigation include:

(1) large-scale spatially explicit representation of aspen abundance;
(2) positive density-dependence at low densities resulting from sibling co-operation during early phase of colony establishment;
(3) non-linear perturbation effect of spring temperature on early larval predation by pentatomids, ants, spiders, carabids - especially in combination with any positive feedback described in (2);
(4) differential effects of fragmentation on host/parasitoid dispersal;
(5) parasitoid post-emergence emigration and re-aggregation in response to spatial variation in host density caused by winter-kill of eggs.
(6) non-linear perturbation effect of temperature on parasitoid competition for hosts through temperature-dependent phenological host-synchrony.

If such landscape-dependent and temperature-dependent stochasticity is insufficient to explain observed patterns of tent caterpillar outbreaks, then it would have to be conceded that the biological details surrounding the host-parasitoid/virus/pathogen interaction probably can not be represented by a simple single-point attractor. In this case, the natural enemy complex should be broken down into constituent processes an modeled separately.

11.3.3.3 Analytical theory

To be truly useful, the non-linear perturbation concept needs to be addressed more formally. A thorough analysis of the statistical properties of theoretical systems governed by non-linear perturbations is required. It may be that analytical approaches to the empirical detection of such effects are not possible and that experimentation and process-oriented simulation is the only alternative. The intractability issue needs to be examined.

Spatiotemporal pattern analysis is in its infancy, and advances are required in order to interpret complex patterns of abundance exhibit by animal populations. Because there are so many parameters that need estimating in a spatiotemporal model, a statistical approach again may be intractable. Ecologists could benefit from theoretical studies indicating the limits of tractability.

APPENDIX 1. A DETAILED GUIDE TO THE PREPARATION OF ASPEN SAMPLES FOR DENDROCHRONOLOGICAL ANALYSIS

A1.1 Drying and sanding sections

Sections should be dried at 40°C for several days. Samples should be placed individually on drying racks in a flat position to facilitate even drying and prevent warping. Sections should be sanded with a table-mounted belt-sander using 15 cm wide 50, 80, and 100 grit belts, and then polished with a palm-sized orbital sander using 150, 220, 320 and 400 grit paper. Annual growth are then easily resolved using a 10-60x magnification stereo-microscope with a variety of light sources.

A1.2 Detecting annual rings

Annual rings in aspen are visible as a sharp transition from dark latewood to light earlywood. Unlike most conifers, this zone is very narrow because latewood formation stops abruptly at the end of the growing season. Upon resumption of growth in spring, a high concentration of large vessel elements are produced and these appear whitish when the section is polished. There is no clear transition from earlywood to latewood because large vessel elements are diffuse throughout the annual growth layer.

A1.3 Cross-dating ring width profiles

Sectional chronologies were cross-dated by examining the cross-correlation among ring width profiles, particularly with regard to high-frequency fluctuations in ring width (Pilcher 1990). When high-frequency fluctuations did not correlate well, samples were re-examined for the possible occurrence of a missing ring or a counting error.

In cross-dating aspen, the importance of visual comparison, especially in the early steps of cross-dating, can not be understated, as there are many attributes of annual rings from a given year that are shared among different stems. These attributes include subtle patterns of variation in colour, texture, and dispersion of large and small vessel elements within the annual growth layer; they are more difficult to quantify than ring width, but their subjective consideration aids the cross-dating process because of the large variation between adjacent rings - a phenomenon that has led to the concept of "pointer years" (Schweingruber 1990).

This concept is useful as long as the spatial extent of sampling does not exceed the scale of synchrony of the disturbance that created the anomalous growth ring. In cross-dating our aspen sections, we resisted the natural temptation to use the occurrence of defoliation-caused white rings as pointer years because assuming synchrony at any scale would bias the results. For example, if outbreaks spread slowly then white rings would act as reliable pointers locally, but not globally; if they occur more patchily, then the scale of utility might only be at the stand level. Thus we chose to assume the scale of utility of white rings as pointer-years was arbitrarily small because the scale of outbreak synchrony might be arbitrarily small. Similarly, prolonged defoliation sometimes leads to several consecutive narrow, intermittent, or missing rings. But these were not used in cross-dating either, as fine-scale spatial variation in defoliation severity over the course of the outbreak should produce varying numbers and patterns of small rings.

A1.4 Measuring ring widths

Unlike annual rings in conifers, which are fairly concentric, aspen rings are often eccentric, apparently as a result of intraspecific competition. Aspen ring widths have unavoidable low-frequency spatiotemporal distortions that seem to result from dynamics within the tree crown and possibly within the local canopy. If only one transect is measured, it must be chosen carefully by avoiding major distortions due to minor wounds and by avoiding intermittent rings. When a transect is found to include a missing or intermittent annual ring, a new transect must be sought where that ring was present. Thus the transects often approximate the largest radius of the section. Also, on rare occasions, such as when it is impossible to avoid both a major low-frequency distortion and an intermittent ring it may be necessary to measure two segments of two different transects. The orientation of these two segments should not differ by more than 10 degrees so that disruptions to the temporal autocorrelation structure will be minuscule. When annual rings are highly eccentric it may be necessary to use a more angular bi-segmented radial transect in order that annual rings be bisected fairly perpendicularly.

A1.5 Scoring white rings

Rings that appear whitish do so because of the disproportionately high number of large vessel elements in the annual ring. There are two ways this proportion tends to vary: an increase in the number of layers of large vessels laid down in the early wood, and a reduction in the width of the late wood. Only rings of the first type should be scored as white. On rare occasions, when a ring is extremely narrow, intermittent or missing, a check should be made on a section from the crown to see if that ring is present further up the bole. If this ring is white, then the lower ring could be scored as white. Many rings that appear whitish with the naked eye do not appear to have the same degree of whiteness or the same cellular structure as others; these should not be scored as white. Also many narrow rings appear whitish merely because they lack latewood growth. These should not be scored as white either, although they frequently occurred the year after a white ring. This scoring policy probably underestimates the incidence of severe defoliation. This is ideal because one would not want to be presumptuous as this technique is fairly new.

A1.6 Literature Cited

Pilcher, J.R. 1990. Sample preparation, cross-dating, and measurement. *In*: E.R. Cook & L.A. Kairiukstis (Editors). Methods of Dendrochronology. Kluwer, Boston, pp. 40-51.

Schweingruber, F. 1990. Dendroecological information in pointer years and abrupt growth changes. *In*: E.R. Cook & L.A. Kairiukstis (Editors). Methods of Dendrochronology. Kluwer, Boston, pp. 277-283.

APPENDIX 2. A ZERO-COST METHOD FOR ANIMATING SPATIOTEMPORAL ECOLOGICAL DATA

A2.1 Plotting maps

Some sort of graphing software is required to map each temporal frame of the ecological data. Options vary from custodial geographic information systems (IDRISI, Arc/Info, etc.) to geostatistical software packages (GS+, GSLIB, etc.) to the most basic contour plotting algorithm available in standard statistical packages (SPSS, SigmaPlot, R, S+, Systat, Minitab, SAS, etc.). The best choice involves a balance between cost, functionality, ease of use, and portability of output. For example, if the data are not on a regular grid, the software must either generate a regular grid by some sort of kriging, or rectify the data internally before graphing.

Depending on how the temporal frames are to be strung together, the map needs to be output in a certain file format. Many graphic programs use proprietary formats and cannot be used as a graphic converter. Graphic converters are available however to convert between any recognizable graphical format (GIF, JGP, PCX, PDF, PNG, EPS, BMP, TIFF, etc.).

Either of two pieces of free software can be used for graphing: PLT, available from the Canadian Forest Service of the Canadian Government, and R (GNU S), available from CRAN. Url's for their sites can be accessed from http://www.ualberta.ca/~bcooke. With either piece of software you can create encapsulated postscript output that can be imported into a commercial graphics package, such as Adobe Illustrator.

To create animations of the forest tent caterpillar defoliation impact data in chapter six, a PLT script file was used to automatically do the following tasks:

(i) import the point data for a temporal frame of spatial observations

(ii) sequentially plot each frame as a 3-D surface or 2-D contour

(iii) annotate the map

(iv) generate an encapsulated postscript (.EPS) formatted map

A2.2 Animating maps

The goal of this step is to create an animated graphic file where each frame of the animation sequence is a temporal frame of the mapped data. This file can be viewed with a web browser or embedded in other applications, such as a slide presentation.

Once a series of maps has been created in a standard graphical format there are several ways to read these and string them together in an animated graphic file. For about $20 GIF Construction Set Professional offers a good "animation wizard" for stringing together all kinds of graphic files into a single animation. A second option is to use the "convert" utility that comes with ImageMagick. Their detailed documentation explains exactly how to use this powerful graphic management tool. Only two ImageMagick commands are needed to convert a sequence of EPS format maps to an animation-friendly format and string them in an animated graphic file. From a DOS window, while in the directory where the convert.exe program resides, execute the commands:

```
convert *.eps gif87:*.gif
convert -delay <d> -loop <l> *.gif animated.gif
```

where <d> is the frame delay in milliseconds, and <l> is the number of times to loop through the sequence. The resulting animation file, "animated.gif", can be viewed in any web browser.

APPENDIX 3. SPATIOTEMPORAL FACTOR ANALYSIS WITH ROTATED PRINCIPAL COMPONENTS

A3.1 Introduction

Spatiotemporal factor analysis is a multivariate statistical method used for identifying and extracting coherent modes of spatial and temporal structure that underlie complex and noisy patterns in univariate spatiotemporal data. The technique has been used successfully to identify climate regions based on distinct patterns of coherence in medium- and low-frequency fluctuations in a variety of meteorological parameters (Karl & Koscielny 1982, Barnston & Livezey 1987). In that literature, the technique is referred to as rotated principal components analysis (RPCA). Richman (1986) reviewed the developmental history of RPCA and its modern application to climatological problems of pattern discovery.

Multivariate spatiotemporal methods have been applied sparingly in the ecological literature - presumably because of the rarity of well-resolved, long-term data. A notable exception is in the area of dendroclimatic reconstruction (*e.g.* Meko *et. al.* 1993, Cook *et. al.* 1999). Here, as in climatological applications, the goal has been the discovery of distinct spatial and temporal modes of variability in tree ring widths that could be explained by meteorological teleconnections. For example: (1) because of ocean-wide convective linkages, ENSO-scale variability in tree ring widths is strongest and most correlated with Pacific sea-surface temperatures around the Pacific rim (Stahle *et. al.* 1998); (2) bi-decadal cycles in tree ring widths are most prominent and most highly correlated with the solar cycle in drought-prone regions of the United States (Cook *et. al.* 1997).

As RPCA has often been used to describe spatial variability in weakly periodic climatological phenomena inferred from tree rings, there is good reason to believe the technique might be helpful in understanding spatiotemporal variability associated with complex patterns of quasi-periodic, quasi-synchronous insect outbreaks.

A3.2 Methods

There are five phases in spatiotemporal factor analysis using RPCA:

1. Recognizing the presence of joint spatiotemporal variability;
2. Deciding on the relevant question and the appropriate mode of analysis;
3. Extracting components of variation;
4. Enhancing simple structure in the extracted components;
5. Interpreting the factors.

Each step will be described briefly in turn.

A3.2.1 Identifying joint spatiotemporal structure

Unlike cluster analysis, factor analysis allows for the possibility that the joint spatiotemporal variation in a pattern sequence may be non-stationary in space and time, as a result of spatially and temporally varying factors. If, for example, outbreak disturbances are governed by dynamic processes, such as climate or self-organization, then groups of stands may slip in and out of synchrony. Thus there may be no one partition that succinctly projects an outbreak sequence onto the temporal domain. Instead, the most parsimonious partition may evolve through time as a trajectory attempts to converge on its attractor but is continually perturbed away from it by environmental fluctuations.

Spatiotemporal factor analysis is particularly useful in the analysis of dendrochronological data because tree ring widths are not only affected by spatiotemporally complex disturbances such as insect outbreaks, they are also largely determined by large-scale climatic fluctuations (Meko *et. al.* 1993, Cook *et. al.* 1999) which tend to be well-synchronized over distances as large as 10^2 to 10^3 km (Cayan *et. al.* 1998). Drought does not spread in the way some insect outbreaks do, and spatiotemporal factor analysis can help to distinguish spreading versus non-spreading components. Thus the technique helps to validate outbreak reconstructions made from tree ring width data.

A3.2.2 Choice of analytical mode

As Richman (1986) describes, the choice of analytical mode is guided by any *a priori* understanding one has about the nature of the generating process, and by examining the source data. A regionalized climatological pattern is best summarized through S-mode analysis. A sequence of spatially complex weather anomalies is best summarized through T-mode analysis. When the generating process is poorly understood and the patterns are ambiguous, either may be appropriate.

A3.2.2.1 Spatial analysis: S-mode

In large-scale, long-term climatological applications, one is typically interested in knowing if there are locations where temporal patterns of weather co-vary similarly through time. Induction of spatial coherence in weather fluctuations is referred to as regionalization (White *et. al.* 1991). Regionalization occurs when local geographic features have a persistent, localized modifying influence on climate patterns, or when there are characteristic statistical modes of atmospheric circulation that influence the large-scale spatial re-distribution of heat and moisture.

If the goal of spatiotemporal analysis is to extract, as independent factors, the various temporal patterns of fluctuations that characterize certain groups of temporally covarying plots, this requires a spatial mode of interrogation (Richman 1986). In an S-mode spatiotemporal analysis, plots are treated as variables (columns) and years are treated as observations (rows). If there are more years than plots, it is possible to conduct an eigenanalysis where each extracted factor corresponds to a different regional mode of variability.

A3.2.2.2 Temporal analysis: T-mode

In some applications, it is desirable to ask the transpose question: which are the time periods when weather maps are highly correlated? If a weather animation indicates, for example, the development and subsidence of a sequence of spatially complex and seemingly unrelated weather anomalies, then the existence of unique non-regionalized modes of spatial variability is more a concern than than the existence of unique regionalized modes of temporal variability (Richman 1986).

To address this transposed problem, a T-mode decomposition is required. Here, years are treated as variables (columns) and plots are treated as observations (rows) and plots should outnumber years. In a T-mode analysis, the objective is to isolate, within each factor, specific types of anomalies. If there are, for example, two or more anomalies that evolve in similar ways, these will load heavily onto a single factor. By identifying unique anomaly-types, it is possible to determine whether they are consistently associated with particular atmospheric conditions. In this way, a complex pattern sequence may be simplified into a more manageable and understandable structure.

A3.2.2.3 Regionalization and punctuation

Two linguistic notes apply here. First, the term "anomaly" is used here in its meteorological sense rather than its statistical sense. A weather anomaly is a distinct and punctuated meteorological event or phenomenon caused by the simultaneous occurrence of a variety of characteristic atmospheric conditions. Because they are determined by the congress of many processes they can be spatially complex. Weather anomalies are anomalous in the statistical sense only when viewed in a small spatial and temporal context. Over sufficiently large spatiotemporal domains, the unusual becomes expected, and weather anomalies are not at all anomalous. Some ecological phenomena, such as environmental disturbances or population eruptions, may similarly be thought of as spatially complex punctuated anomalies.

Second, although spatial coherence of temporal fluctuations over regional scales is often referred to as "regionalization" (*e.g.* Richman & Lamb 1985, White *et. al.* 1991), there is no comparable term for temporal coherence in spatial variability over a given time horizon. The term "punctualization" would capture the idea of a transition to coherence, but here the degree of punctuality is undefined.

The fundamental problem is that there are no words in the English language to distinguish between small and large portions of time in the way one can readily distinguish between small and large portions of space using the terms "local" and "regional". In ecological contexts, "regional" refers to something less than the size of the globe, and often less than the size of a continent (*e.g.* 100 to 1000 km) while "local" usually refers to something greater than the size of a human organism, but less than regional (*e.g.* 1 to 10 km).

In chapter five, the terms "global" and "local" were used in a temporal context to describe Lyapunov exponents calculated over short and large time horizons. Although these terms usually imply spatial dimensionality, any ambiguity there was avoided by the fact that the temporal connotation was obvious by context, and scale could be inferred from the length (100 y) and resolution (1 y) of the time-series. In the current situation, however, where time is not finite, the term "global" is undefined and the term "local" is therefore ambiguous. How, then should one distinguish between a process that is sharply punctuated versus one that is vaguely punctuated? And how would one describe the transition from uncorrelated spatiotemporal noise to punctuation?

A3.2.2.4 Ecological duality

In many ecological applications, both spatial and temporal analytical modes may be relevant because disturbance pattern sequences may exhibit either regional or punctual structure. In fact, some disturbances, such as wildfire and insect outbreak, can exhibit both kinds of patterning simultaneously. Spatiotemporal variability in these types of disturbance regimes is a result of: (1) spatial variation in landscape features; (2) temporal variation in climatic conditions, and (3) joint spatiotemporal variability associated with autocatalytic spread. The last of these components is not as important in meteorological applications, although some meteorological phenomena, such as hurricanes, are thought by some to originate and subside though autocatalytic means (Pfeffer & Challa 1992, Gray 1998).

A3.2.3 Extracting components of variation

The first benefit of spatiotemporal factor analysis is that each mode of variability is attributed a variance, such that individual modes can be objectively compared in terms of the amount of spatiotemporal variation they engender. In S-mode analysis, the objects of comparison would be regionalized fluctuation-types. In T-mode analysis, the objects of comparison would be punctuated anomaly-types.

Secondly, by decomposing the total spatiotemporal variation in terms of additive components it is possible to determine how the various modes might relate to driving environmental variables. In a disturbance-modeling application, for example: (1) regionality in fluctuation-types may be induced by static regional landscape features (*e.g.* forest structure, hydrology, climatic gradients); (2) punctuality in anomaly-types may be induced by stochastic environmental perturbations; (3) spatiotemporal patterns of disturbance growth, spread and collapse may vary in time and space as a result of autocatalytic processes or self-organization.

A3.2.4 Enhancing simple structure

The notion of simple structure is based on the principles laid out by Thurstone (1947) (Richman 1986). Briefly, simple structure means that plots close together tend to fluctuate similarly (regionalization, addressed by S-mode) or years close together tend to be patterned similarly (punctuation, addressed by T-mode). Of course, ultra-simple structure (regionalized and punctuated) is equivalent to synchrony while non-simple structure (non-regionalized, non-punctuated) is equivalent to randomness, and neither have the simple structure that is well-suited to spatiotemporal factor analysis. In the first case, nearly all the variation will be accounted for by the first factor. In the latter case, no factor will account for much variation and any apparent structure would be spurious.

Orthogonal, unrotated solutions derived from factor analysis provide more the most efficient method for summarizing spatiotemporal variability in a univariate dataset; however, for the purposes of factor interpretation, rotated solutions are often better. Rotation tends to enhance any simple spatial and temporal structure present in meteorological and climatological data (Richman 1986, White *et. al.* 1991).

Different types of rotations vary in their effectiveness at enhancing simple structure. Two of the most commonly used rotations are based on varimax and promax criteria (Richman 1986). Both are widely available in commercial and non-commercial statistical software packages. Briefly, varimax rotation is an orthogonal rotation that seeks to maximize the dispersion of factor loadings by maximizing the number of large and small coefficients in the rotated loading matrix. Promax rotation has the same objective, but without the orthogonality constraint.

To test if a particular rotation has successfully simplified the structure of an unrotated solution, Richman (1986) recommended a visual inspection of pairwise plots of factor loadings. Simple structure is indicated when loadings are distributed tightly along component axes. If loadings scatter in a cloud of points, simple structure has not been extracted.

A3.2.5 Interpreting factors

Factors derived from decomposition can be used in environmental correlation analysis and spectral analysis. If, for example forest fragmentation is an important factor that increases the frequency of outbreaks, then one would expect at least one factor to be temporally characterized by strong periodicity of a given frequency and spatially correlated with forest structure. If large-scale winter weather anomalies have a strong impact on temporal outbreak dynamics, one would expect at least one factor to relate temporally to winter temperature and spatially to microclimatic vulnerability. Of course, there is a limit on the forms of joint spatiotemporal structure that can be inferred when sample points are highly aggregated in space with large gaps between them.

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